

# ECOGRAPHY

## Research article

### Species accumulation in novel grassland habitats is linked to land cover history

Svenja Horstmann<sup>1</sup>✉, Alistair G. Auffret<sup>1</sup>, Juliana Dániel-Ferreira<sup>2</sup> and Erik Öckinger<sup>1</sup>

<sup>1</sup>Swedish Univ. of Agricultural Sciences, Dept of Ecology, Uppsala, Sweden

<sup>2</sup>Swedish Univ. of Agricultural Sciences, Swedish Biodiversity Centre, Uppsala, Sweden

Correspondence: Svenja Horstmann ([svenja.horstmann@slu.se](mailto:svenja.horstmann@slu.se))

#### Ecography

2023: e06704

doi: [10.1111/ecog.06704](https://doi.org/10.1111/ecog.06704)

Subject Editor: Henrique Pereira

Editor-in-Chief: Miguel Araújo

Accepted 31 March 2023



Novel grassland habitats along linear infrastructure have gained attention as potential supplementary or replacement habitats for species suffering from the widespread loss of traditionally managed semi-natural grasslands. However, it can take time for species to colonise new habitats, and both the historical and the current landscape composition can affect colonisation rates, particularly for grassland specialist species. We investigated the influence of more than 100 years of landscape history on present-day species richness of plants, butterflies and bumblebees in two types of linear infrastructure habitats: road verges and power line corridors. We analysed the effects of time since habitat establishment and the amount of surrounding grassland cover in different time periods on species richness of the three taxa. Our results suggest a long time lag in the establishment of plant species in novel grassland habitats, with richness of butterflies and bumblebees largely dependent on the richness of plant species. There was no direct relationship between habitat age and the richness of butterflies or bumblebees, but we found unexpected legacy effects of grassland area on present-day species richness. Higher richness of bumblebee species in road verges located in landscapes with larger surrounding grassland cover in the past is most likely a consequence of those landscapes containing a mosaic of afforested and abandoned grassland habitats today. Furthermore, we found that power line corridors might be important replacement habitats for butterflies in landscapes with little other grassland area left. Provided that road verges and power-line corridors are managed appropriately, our results show that their species richness can be expected to increase in the future.

Keywords: landscape history, linear infrastructure, pollinator, power line, road verge, vascular plants

#### Introduction

Semi-natural grasslands that have been managed through low-intensity grazing or mowing for centuries host diverse plant and insect communities and are one of the most species rich habitats in Europe (Cousins and Eriksson 2002, Wilson et al. 2012).

© 2023 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.



[www.ecography.org](http://www.ecography.org)

However, starting around the turn of the 20th century, intensive agriculture displaced traditional management across the continent (Eriksson et al. 2002). Improved farming methods including artificial fertilizers and the increased production of ley and grain on fields led mainly to the abandonment of many semi-natural grasslands or to their conversion to forest (Eriksson et al. 2002, Cousins et al. 2015, Auffret et al. 2018). Yet at the same time as historical grasslands have been lost, new grassland habitats are emerging along linear infrastructure. These managed, open areas along roads, railways and power line corridors have gained attention as potential replacement habitats for species suffering from the loss of traditionally managed semi-natural grasslands (Berg et al. 2016, Phillips et al. 2020, Vanneste et al. 2020). Such habitats are largely kept open for safety reasons, but the resulting open vegetation provides grassland habitats that at least to some extent resemble traditionally managed semi-natural grasslands (Gardiner et al. 2018). Road verges provide habitat for grassland specialist plants (Vanneste et al. 2020) and act as hotspots of pollinator diversity (Phillips et al. 2020). Both road verges and power line corridors can sustain a richness and abundance of bumblebees comparable to semi-natural grasslands (Hill and Bartomeus 2016), and power line corridors can even be a source habitat for butterflies (Berg et al. 2016). As these habitats cover large areas, they provide an opportunity to preserve grassland biodiversity in human-dominated landscapes (Wojcik and Buchmann 2012, Gardiner et al. 2018). However, it is unclear whether these novel grassland habitats have had the time to accumulate a diversity similar to that in their older counterparts, and whether this accumulation depends on the amount of core habitat in the surrounding landscape, particularly with regard to interactions between plants and pollinators.

Changes in local land use, management, or connectivity to other habitat patches in the landscape can alter diversity accumulation and structure in both the short and long term. Although some changes such as habitat loss or degradation can immediately affect local diversity, the full response to change is often apparent after a delay, resulting in an extinction debt (Kuussaari et al. 2009). This can be either because individuals and local populations persist for some time even after local conditions have become unsuitable, or because metapopulations can survive long after the balance between local extinctions and (re)colonisations is altered (Hanski and Ovaskainen 2002, Hylander and Ehrlén 2013). This landscape legacy effect has for example been observed for plants and butterflies, where current diversity was better explained by historical than by present cover and connectivity of semi-natural grasslands (Bommarco et al. 2014). The time lag in local extinction of species that are not in equilibrium with their environment implies a future decline of diversity even if current environmental conditions remain stable (Jackson and Sax 2010, Bommarco et al. 2014). Time lags can also occur in the assembly of target communities following habitat creation or restoration, such that there is a colonisation credit (Watts et al. 2020). The successful (re-)colonisation by

target species is broadly determined by the ability of species to disperse to, and establish in, new habitat patches (Hanski 1999). This in turn is often limited by landscape factors, because the amount and configuration of nearby habitat can determine how easy a species can move in space (Tischendorf and Fahrig 2000). As such, species diversity can be expected to increase when connectivity between habitats increases (Damschen et al. 2019), and this has broadly been shown in novel habitats such as road verges and power line corridors (Lampinen et al. 2018, Auffret and Lindgren 2020).

Responses to landscape composition and configuration vary across taxonomic groups – grassland specialist plants – whose effective dispersal relies almost entirely on external factors such as landscape connectivity and presence of dispersal vectors – often exhibit very slow colonization rates, especially in fragmented landscapes with little suitable habitat (Helsen et al. 2013, Auffret et al. 2017c, Damschen et al. 2019). Mobile species with short generation times, such as flying insects, are often able to react more rapidly to habitat changes (Kuussaari et al. 2009), and hence their diversity is more likely to already be in balance with the current landscape connectivity (Krauss et al. 2010). Nonetheless, herbivorous and pollinating insects depend on the sufficient availability of certain plants. This dependence on plant community responses means that pollinator arrival to a new habitat may be indirectly delayed (Krauss et al. 2010). Hence, time since habitat establishment and the amount of surrounding source habitat are likely to be important drivers for the species accumulation in novel grassland habitats, especially for grassland specialists. However, studies on landscape legacy effects on plant and insect diversity in linear infrastructure habitats are limited and conflicting. Auffret and Lindgren (2020) found no effect of either historical or current surrounding grassland cover on plant richness in road verges. In power line corridors, historical connectivity to grassland habitats was shown to increase the richness of plant species, but there is less evidence of a relationship between historical or current connectivity and butterfly richness (Lampinen et al. 2018).

In this study, we investigated the effects of historical land cover and habitat age on species accumulation of vascular plants, butterflies and bumblebees in novel grassland habitats along roads and power line corridors. We ask 1) if increasing habitat age leads to a local species accumulation of vascular plants overall and grassland specialist plants especially, and 2) if habitat age affects faster dispersing taxa such as butterflies and bumblebees. Considering present and historical land cover, we also ask 3) how the surrounding grassland cover from the past or the present affects local species richness. Since we lack sufficient knowledge on how historical or current land cover affects species accumulation, we used a combination of ecological model formulation approaches and statistical optimization methods to find the most relevant predictor variables for each taxon. Also, by investigating plants and flower-visiting insects in the same study design, we were able to assess how these interacting species groups react to the establishment of novel infrastructure habitat.

## Material and methods

### Study area

To select study landscapes, we first created  $2 \times 2$  km landscape grids over the counties of Uppsala, Stockholm, Södermanland and Västmanland in Sweden and selected landscapes that were dominated by forest (45.2–81.2%) and had a gradient in the cover of semi-natural grasslands (0.8–9.9%) (Supporting information). Additionally, we filtered for contrasting road densities (low density: average of 4.9 km, high density: average of 16.3 km), and presence ( $n = 16$ ) or absence ( $n = 16$ ) of a power line corridor of at least 1 km length and surrounded by forest. This allowed us to select 32 landscapes (i.e. grids of  $2 \times 2$  km) with contrasting road density, presence versus absence of power line corridors, and a gradient in the area of semi-natural grasslands (Dániel-Ferreira et al. 2020). We previously used this study design to describe effects of the presence or absence of power line corridors and road density on landscape scale diversity of plants, butterflies and bumblebees (Dániel-Ferreira et al. 2020), and on the differences of alpha and beta diversity of the species groups between the different habitats (Dániel-Ferreira et al. 2023). For the current study, we used a subset of this data, i.e. from one road verge along a small gravel road, one road verge along a larger paved road and one power-line corridor (in the 16 landscapes with power line corridors present) within the 32 landscape grids. We did not include road density, since this information was only calculable for the present but not the historical landscapes. From each of these habitats, we used data on the diversity of plants, butterflies and bumblebees, collected in 2016.

In the study region, power line corridors are managed by clearing shrubs and young trees every eight years, hence maintaining an early-successional vegetation. The power line corridors in our study had been cleared between 0 and 6 years prior to the biodiversity surveys, with a median of 2.5 years for all power line corridors. The power line corridors were between 28 and 95 m wide, with an average width of 39.9 m. Road verges in Sweden are typically mown once or twice per year and cuttings are usually not removed. All road verges were at least 1.5 m wide. Verges along gravel roads had a maximum width of 5 m and an average width of 2.8 m, and verges along paved roads had a maximum width of 5.5 m and an average width of 2.9 m.

### Plant and insect surveys

In each study site, we separately surveyed plants, butterflies and bumblebees along a 200 m long transect. For the plants, we placed four  $1 \times 1$  m plots along each transect, separated by a distance of 50 m. In every plot, we recorded the presence or absence of all plant species from a pre-defined list of 169 species, all of which are frequently occurring in various types of grassland habitat in the study region. The list contained the absolute majority of the species present across all sites. The plant inventory was carried out once per site between 13 July and August 24 in 2016. Walking slowly along the

same transects, we identified and counted all butterflies and burnet moths (Zygaenidae; from here on included in 'butterflies') within 2.5 m to each side and 5 m to the front of the observer. For narrower road verges, we counted all individuals along the transects. Burnet moths are diurnal and were included among butterflies because they have similar habitat requirements. We surveyed bumblebees along the same transects but within 1 m to each side and to the front. We caught and identified individuals in the field if possible or collected and identified them in the laboratory. No bumblebee queens were collected to avoid impacts on respective populations. We surveyed butterflies and bumblebees each four times per site, between 1 June and August 23 in 2016. To avoid observer bias, the surveyors inventoried all habitats and to reduce bias due to activity patterns of the insects during the day, the order of sites visited on the same day was randomized. The surveys were only conducted on days with dry vegetation, temperatures above 17°C when sunny and above 20°C when cloudy and only between 10:00 and 16:00 h.

For butterflies and plants, we calculated the richness of grassland specialists and the total richness of all species, according to the classifications in Öckinger et al. (2012). Any species that occurred in our study but were not included in this list were classified according to our knowledge (Supporting information). Because bumblebees forage in a wide range of habitat types, we did not attempt to classify them into grassland specialists and only calculated total richness (Supporting information).

### Current and historical land cover

We used maps of two time periods to calculate current and historical grassland cover, in a 2 km radius around each of the surveyed road verges and power line corridors (Fig. 1). Previous studies found effects of historical land cover on the 2 km scale on the studied taxa in semi-natural grasslands (Lindborg and Eriksson 2004, Krauss et al. 2010, Bommarco et al. 2014). Creating individual buffers around each study site meant that buffers included land outside of the initial landscape grids, but allowed us to get site-specific estimates of current and historical land cover in the respective surroundings. Buffers around the three habitats within each landscape grid overlapped, and in two cases buffers around the same habitat type of two separate landscape grids overlapped (with 7.1 and 12.2%; see below for how this was accounted for in the analyses). For the historical land cover, we used published digitisations of the 1940s–1960s Swedish Economic Map (Ekonomiska kartan, hereafter '1950s map') (Auffret et al. 2017a,b). Digitisations show land cover in four categories at a resolution of 1 m; arable, forest, grassland (mostly consisting of semi-natural grassland habitat, but also includes other open land cover types, such as wetlands and urban land uses; cf. Auffret et al. 2018) and surface water. For the current land cover, we used the National Land Cover Database (Nationella marktäckedata) showing land cover data of Sweden from 2017 to 2019 (Naturvårdsverket 2020) (hereafter '2017 map'). This database classifies Sweden into 25 categories of land cover (of

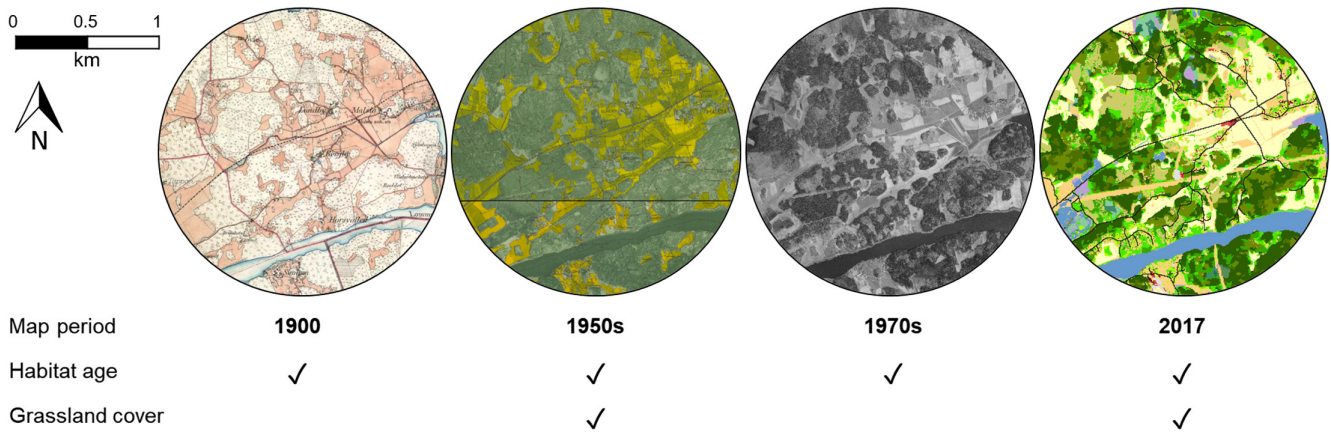


Figure 1. Overview of the four maps used to assess linear infrastructure habitat age and grassland cover in a 2 km buffer (represented) in different time periods. Pictures of maps show the original; the 1950s map was digitised and the land cover categories of the 1950s and 2017 map were reclassified before analyses.

which 16 are various types of forest) at a resolution of 10 m. These more detailed land cover types were grouped to fit to the four broader land cover types of the 1950s map (Supporting information), while we aggregated and resampled (nearest neighbour) the pixels in the 1950s map to match the grid of the 2017 map in R (package ‘raster’: Hijmans et al. 2022, [www.r-project.org](http://www.r-project.org)). We then created a 2 km buffer around the start coordinates of the transects used in the diversity survey (package ‘rgdal’: Bivand et al. 2021a, package ‘rgeos’: Bivand et al. 2021b), calculating the proportion of grassland within each buffer at each time period. Because the 2017 map does not differentiate species-rich semi-natural grassland from other grassland types, we additionally calculated the proportion of pixels within each buffer that was classified as grassland both in the 1950s and in the 2017 maps (hereafter ‘continuous grasslands’).

### Habitat age

To define the age of the studied linear infrastructure habitats, we used four points in time (Fig. 1). In addition to the two maps we used for the land cover calculations (from the 1950s and 2017), we also used two other non-digitised sources: geo-referenced aerial photographs, taken between 1970 and 1976 (‘1970s map’), and a historical map created between 1859 and 1911 for our landscapes (Häradsekonomska kartan, ‘1900 map’). We manually examined in which map a respective contemporary infrastructure habitat appeared for the first time and grouped all respective habitats into four categories corresponding to the four points in time (Supporting information). Some roads changed course slightly over time, but were categorised as present if the majority of the stretch overlapped. We have no knowledge on the exact management history of our road verges, but assume that the vegetation has always been kept relatively open. Furthermore, although the time periods between available maps and aerial photographs differ in their distance, the points in time represent relevant time periods for the land use change in Sweden (Eriksson et al. 2002, Cousins et al. 2015) and the creation

and expansion of power line corridors and road networks. All map sources except the 1900 map were geo-referenced and the habitats were examined using QGIS ver. 3.10 (QGIS.org 2020). For the 1900 map, we manually located the contemporary habitats using unaltered landmarks.

## Data analysis

### Statistical approach

We investigated the effects of habitat age and surrounding grassland cover on the richness of plants (total richness and number of specialist species), butterflies (total and specialists) and bumblebees (total only) in two prevalent grassland habitats: road verges and power line corridors. Given their relevance to our questions, habitat age and surrounding grassland cover were fixed predictors in all models. Because landscape grassland cover from different time periods can have smaller or larger effects on species richness in novel habitats depending on the infrastructure habitat and taxon in focus (Lampinen et al. 2018, Auffret and Lindgren 2020, Dániel-Ferreira et al. 2020), we wanted to include the most relevant landscape predictor (surrounding grassland cover in 1950s, 2017, or continuous) in each of our ten models. These values were non-independent and correlated (highest  $|r_{\text{pearson}}| = 0.77$ , Supporting information), and so we used a statistical approach using single-predictor models to select which grassland cover was the best predictor for each species group in each habitat.

### Single-predictor models

We built a suite of single-predictor GLMs to determine the predictive power of each of the three candidate grassland cover variables individually for each of the five species groups in the two novel habitat types (cf. Auffret et al. 2018, total 30 models; Supporting information). Within each species group-habitat combination, we calculated the R squared value for each model (package ‘rsq’: Zhang 2021, [www.r-project.org](http://www.r-project.org)),

with the surrounding grassland cover measurement explaining the most variation in species richness in each case being selected for the final model. Since insect richness can depend on plant species richness, for each of the insect models we included either grassland specialist or total plant richness as a potential predictor variable. Because these were also highly correlated ( $|r_{\text{Pearson}}|$  between 0.90 and 0.95; Supporting information) we also created single-predictor GLMs to determine which plant richness variable had a higher predictive power for the respective insect groups within each habitat type (six models; Supporting information).

## Full models

We created ten full models, which had total or grassland specialist richness of our three species groups in the two infrastructure habitats as a response variable. All models had the following fixed predictor variables: 1) habitat age and 2) surrounding grassland cover as determined from the single-predictor models. All insect models also included 3) total or grassland specialist plant richness as determined from the single-predictor models. To account for spatial autocorrelation, we calculated the Moran's I autocorrelation coefficient using an inversed distance matrix (package *ape*: Paradis and Schliep 2019, Supporting information). For models including spatially autocorrelated data (i.e. where Moran's I was significant at the 0.05 level), we therefore included 4) the first axis of a principal coordinates of neighbour matrix (PCNM) as an additional fixed predictor variable (package *vegan*: Oksanen et al. 2020). Road verge models also included 5) the type of road (gravel or paved), as well as a random effect for landscape identity, since each study landscape contained two road verge study sites (one of each type). Gravel roads were mostly younger than paved roads, but there was no correlation between road type and habitat age. Models for power-line corridors were generalised linear models (GLM), while for road verges we used a generalised linear mixed modelling approach (GLMM) due to the random effect for landscape identity.

## Model selection

All ten models were built as a full model with all relevant predictor variables, before we performed a backwards model selection to determine the best-performing model. 1) Habitat age and 2) surrounding grassland cover were set as obligatory fixed factors, as well as 3) the PCNM if applicable. There was no collinearity among the final predictors that could be expected to considerably interfere with model selection or prediction in any of the models (highest  $|r_{\text{Pearson}}| = -0.53$  and 0.25) (Dormann et al. 2013, Supporting information). We used the Akaike information criterion for small sample sizes (AICc) to select the final predictors for every model and to test for the importance of two-way interaction effects between all variables (package *MuMIn*: Barton 2022, Supporting information). However, due to model convergence issues, interactions between 2) surrounding grassland

cover and 5) road type and between 1) habitat age and 5) road type were excluded. If multiple models were selected with  $\text{AICc} < 2$ , we chose the model with the lowest AICc. For the final models, we conducted model diagnostics using fitted versus residual plots, Q-Q plots ('stats' package: base R, [www.r-project.org](http://www.r-project.org)) and additional overdispersion tests (package 'performance': Lüdecke et al. 2021). To account for overdispersion when needed, we included an observation-level random effect, and for under-dispersed data we used mean-parameterized Conway–Maxwell–Poisson distribution (package *glmmTMB*: Brooks et al. 2017). For the final models we conducted pairwise comparisons for each combination of habitat age categories, using Tukey-adjusted p-values (package *emmeans*: Lenth et al. 2022, Supporting information).

## Results

Overall, we recorded 121 plant species of which 70 were classified as grassland specialists, 49 butterfly species including 22 grassland specialist species, and 18 bumblebee species (Supporting information). The cover of surrounding grassland in the 1950s varied between 0.3 and 28.7%, with an average of 10.5% (Supporting information), while in 2017 there was an overall mean of 15.7% of grassland cover, varying between 5.1 and 15.7%. Despite this apparent increase, less than one fifth of the surrounding grassland cover in 2017 was continuous grasslands that already existed in the 1950s (on average 2.9% of the landscape).

In general, the difference in explanatory power between the single-predictor models comparing the different grassland cover variables was quite small (between 0.001 and 0.029, Supporting information). Nonetheless, in nine out of ten cases the most informative variable was related to historical land use, being either 1950s grassland cover or grassland cover that has been continuous since the 1950s. Butterflies in power line corridors were the exception to these findings, with both total and specialist richness showing the most variation in explanatory power across the single-predictor models.

## Plants

The total plant species richness in road verges was on average 47.3% higher along historical roads already existing in 1900 than along roads only established before 2017 (Fig. 2A). For grassland specialist richness, we found no difference between road verges of different ages (Fig. 2B). The total and specialist plant richness was higher along gravel roads than along paved roads (Supporting information). In power line corridors, the total plant species richness tended to be higher in habitats first appearing in the 2017 map than in those already existing in the 1970s (Fig. 2C). Corridors that already existed in the 1950s had on average 65.8% more specialist plants than those that first appeared in the 1970s (Fig. 2D). The respectively selected grassland cover in the surrounding landscapes did not affect the total or specialist plant species richness, neither in road verges nor in power line corridors. In the single-predictor

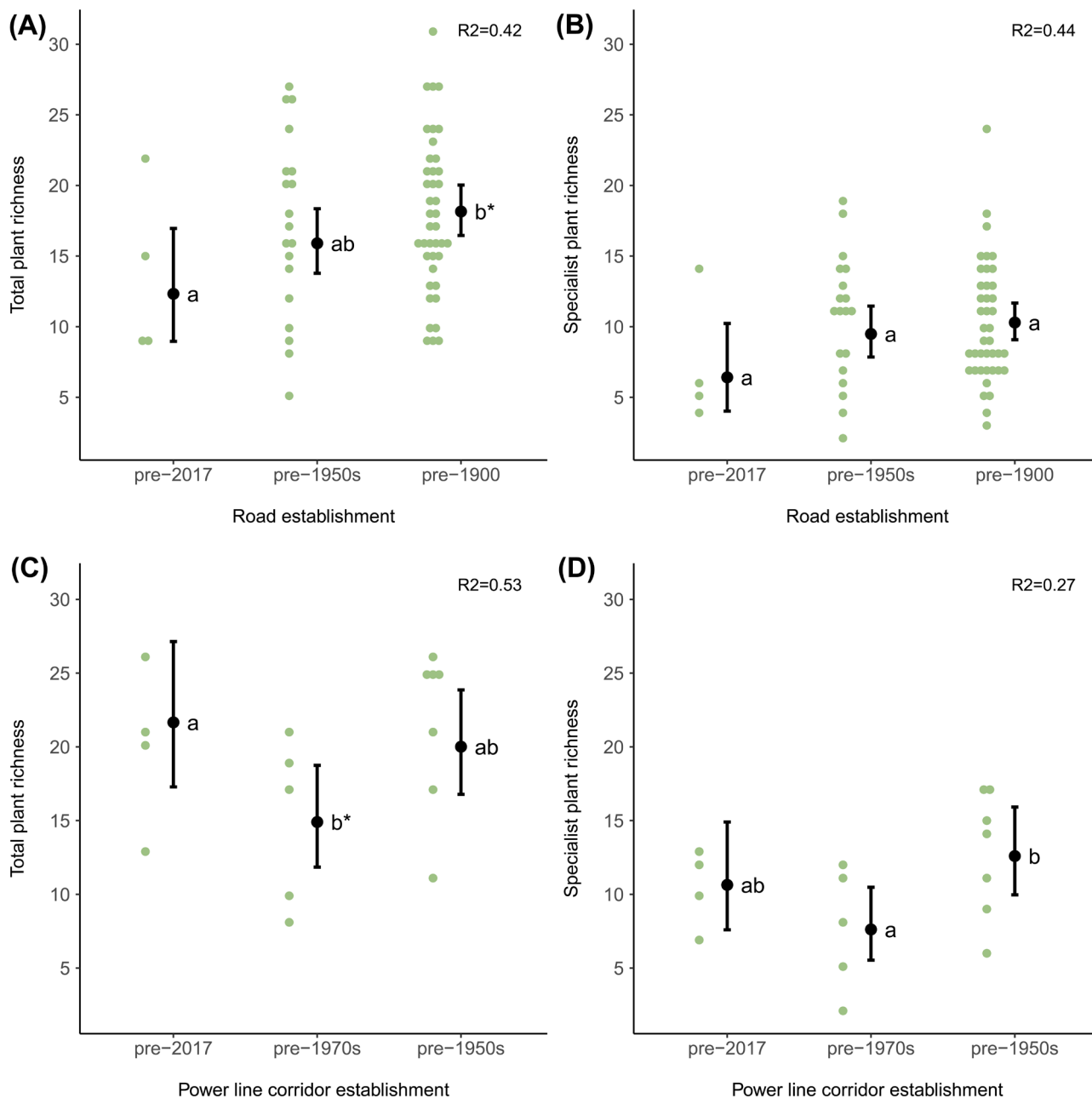


Figure 2. Effect plots for the relationship of habitat age and the richness of (A) all plant species and (B) grassland specialist plant species in road verges, and (C) all plant species and (D) grassland specialist plant species in power line corridors. Green dots represent raw data. Black dots show the predicted value of the estimated mean richness, error bars indicate the 95% confidence interval of the predicted mean. Means sharing a letter are not statistically different ( $p < 0.05$ ), asterisk letters show marginal statistical differences ( $p < 0.07$ ) (Tukey-adjusted pairwise comparisons).

analyses, the potential grassland cover variables showed a low difference in explanatory power (Supporting information).

### Butterflies and bumblebees

We found a strong positive relationship between the richness of specialist plant species and the richness of butterfly species in road verges, for both the grassland specialist butterflies (Fig. 3A) and the total butterfly species richness (Supporting

information). Furthermore, specialist and total butterfly species richness were highest in road verges first appearing in the 2017 map (Supporting information), with around 50% fewer total butterfly species in road verges from before 1900 and the 1950s than in road verges first appearing in the 2017 map. In power line corridors, there was no relationship between habitat age and total butterfly species richness or specialist butterfly species richness. Surprisingly, the number of specialist butterflies was negatively related to the cover of

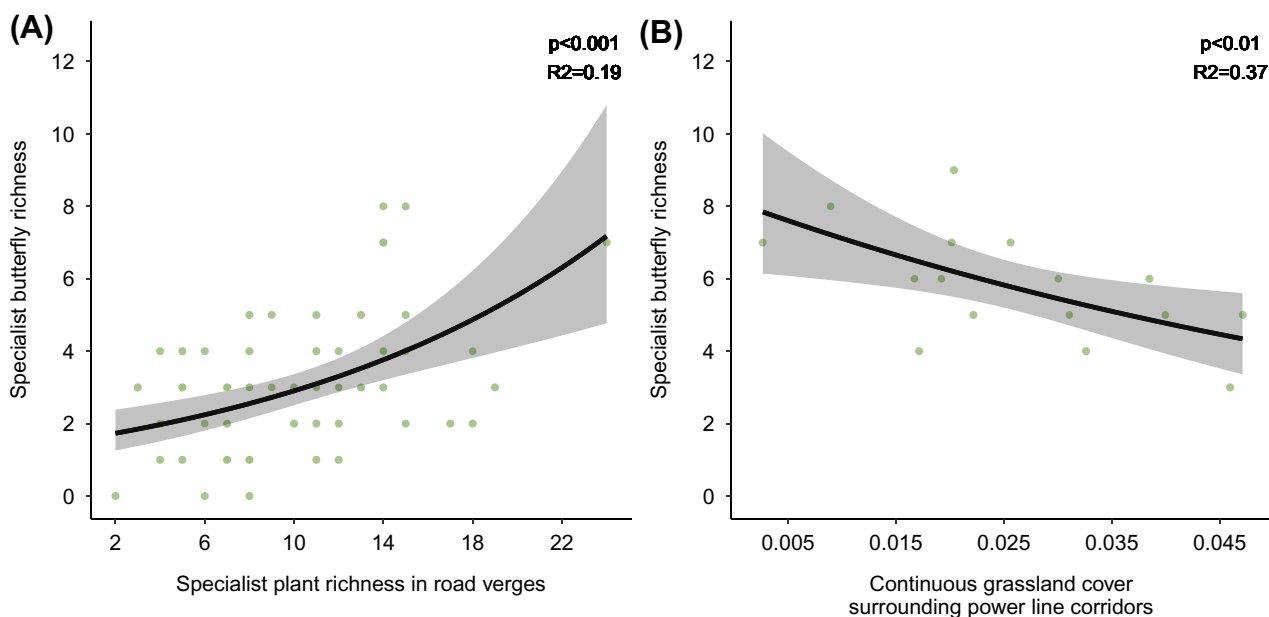


Figure 3. Effect plots for grassland specialist butterfly richness in two different infrastructure habitats, depending on (A) the richness of specialist plants in road verges and (B) the proportional cover of continuous grassland surrounding power line corridors. Green dots represent raw data. Black lines show the predicted value of the estimated mean richness, grey areas indicate the 95% confidence interval of the predicted mean richness.

continuous grasslands around power line corridors (Fig. 3B), and the total butterfly richness negatively related to the cover of current grasslands in 2017 (Supporting information). The difference in explanatory power between potential surrounding grassland cover variables was high for power line corridors but lower for road verges (Supporting information).

For bumblebees in road verges, there was a strong positive relationship with the total richness of plants, as well as with the surrounding grassland cover from the 1950s (Fig. 4A–B). We found no relationship between habitat age and bumblebee species richness in road verges, but in power line corridors bumblebee species richness was higher in corridors first

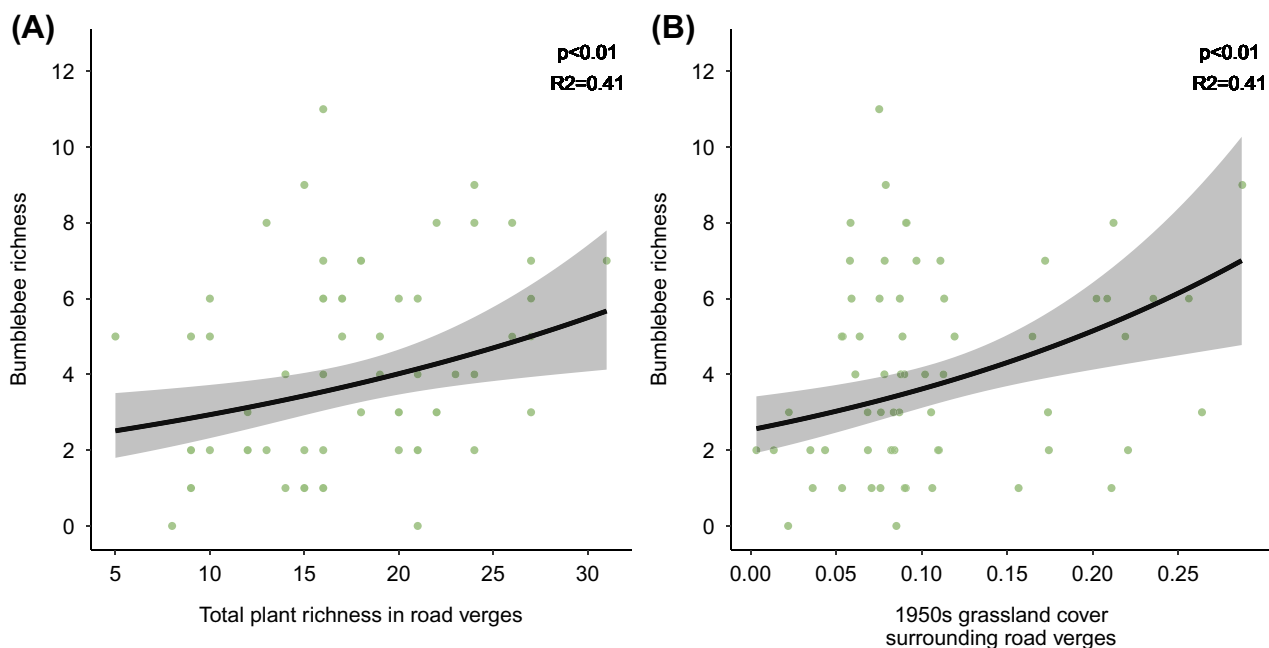


Figure 4. Effect plots for the bumblebee species richness in road verges, depending on (A) the richness of total plants and (B) the proportional cover of grasslands in the 1950s in the surrounding landscape. Green dots represent raw data. Black lines show the predicted value of the estimated mean richness, grey areas indicate the 95% confidence interval of the predicted mean richness.

appearing in the 2017 map compared to those visible in the 1970s map. The difference in explanatory power between potential grassland cover variables was low for both habitats (Supporting information).

## Discussion

Our study shows that in general, both habitat age and landscape history can be drivers of contemporary species richness in linear infrastructure habitats. However, the effects differed between road verges and power line corridors, as well as among plants, butterflies and bumblebees. We found more plant species in older linear infrastructure habitats, and road verges with a higher plant species richness supported higher numbers of both butterfly and bumblebee species. In power line corridors, butterfly species richness was driven by landscape effects rather than by local resource availability.

Our results provide evidence that the accumulation of plant species in a novel grassland habitat can take a long time. In road verges, the overall plant species richness was higher along historical roads that already existed in 1900 than along young roads that first appeared on the 2017 map, with intermediate levels of species richness along roads constructed in the intervening period. This result concurs with [Auffret and Lindgren \(2020\)](#), who found plant richness to be highest in verges along roads that are older than 100 years. For power line corridors, we found a higher number of specialist plant species in older habitats, i.e. in those that were established before the 1950s compared to before the 1970s. [Lampinen et al. \(2015\)](#) also found that specialist plant species richness increased with power line corridor age, even when looking back < 50 years. Due to the construction of electricity networks mainly in the 20th century, it was unfortunately not possible to study the relationship between plant species richness and landscape composition further back in time. It should be noted that even though the time periods between the maps were of different length, this does not affect our main conclusions, since our aim was not to quantify the exact length of time lags in species accumulation. For semi-natural grasslands, the positive effects of long-term continuous management of mowing or grazing on plant diversity are well-established ([Cousins and Eriksson 2002](#), [Gustavsson et al. 2007](#), [Eriksson 2013](#)). Although we have no knowledge on the exact management history of our infrastructure habitats, we assume that the vegetation has always been relatively open, and that the long-term, low-intensity management of road verges has benefitted plant richness. Based on our results, we expect that plant species richness will further increase with advancing time since establishment of linear infrastructures, if current conditions remain. However, it may take over a century to see significant differences.

We found no relationship between continuous or historical grassland cover on plant species richness in linear infrastructure habitats. Nearby grasslands could in theory act as source habitats for colonization to novel habitats ([Helsen et al. 2013](#), [Damschen et al. 2019](#)), while high levels of historical

grassland cover might indicate the existence of remnant communities despite losses in core habitat ([Lindborg and Eriksson 2004](#), [Scherreiks et al. 2022](#)). However, < 3% of the landscape surrounding our infrastructure habitats consisted of grassland habitat that has existed since the 1950s. This could help explain why the increase of plant species richness in the studied infrastructure habitats is slow, and raises the question of whether a larger area of continuously available high-quality grassland in the surroundings would enable a more efficient colonization of road verges and power line corridors. It is possible that the assembly of grassland communities in our study habitats was based on low-frequency long-distance dispersal events that could not be predicted by the landscape immediately surrounding the target site ([Trakhtenbrot et al. 2005](#)).

From a community-assembly point of view, it was surprising that the total plant richness tended to be lower in power line corridors established before the 1970s than pre-2017. Nonetheless, this was not the case for grassland specialists, and we can only speculate that this might be due to a decline in species adapted to forest conditions that existed before the creation of the corridors. Although all studied power line corridors are currently surrounded by forest, several of them had previously been pastures that were later afforested, a common trend in Swedish landscapes ([Cousins et al. 2015](#)). Previous work has indicated that relatively high richness in some power line corridors could be the result of time-lagged extinctions from previous land uses ([Lampinen et al. 2018](#)), and that power line corridors might even contribute to the maintenance of landscape-scale grassland biodiversity ([Daniel-Ferreira et al. 2020](#)). These findings and the results of our study highlight the importance of older power line corridors and their appropriate vegetation management, in order to retain the plant species in the long term.

By combining plants, pollinators and herbivores in the same study, we were able to assess how these interacting species groups react to land use changes. In road verges, the number of butterfly and bumblebee species were positively related to the richness of plant species. Other studies have found that road verges can support an abundance and richness in both flowers and pollinators comparable to or higher than in semi-natural grasslands ([Phillips et al. 2020](#)). In our study, the overall and specialist butterfly richness increased with the number of grassland specialist plant species, which likely reflects the presence of a range of nectar and host plants. This relationship between the plant and butterfly richness was also found by [Ekroos et al. \(2013\)](#). Thus, we can expect that road verges with a higher richness of specialist plants can support more butterfly species with diverse requirements. Bumblebee species richness was positively related to total plant species richness, probably because bumblebees respond to the general availability of various forb species ([Steinert et al. 2020](#)). This is supported by the observation that road age was not a significant predictor for bumblebee richness, even though total plant richness increases with age. We also found that the number of bumblebee species in road verges positively relates to the proportion of grasslands from the 1950s. Swedish landscapes previously dominated by open habitat have



undergone a large-scale increase in forest cover and abandonment of grasslands (Cousins et al. 2015, Auffret et al. 2018). We therefore suspect that landscapes that had a larger area of grasslands in the past are composed of a mosaic of higher forest cover and different-aged, abandoned grasslands today, and that this heterogeneous landscape promotes bumblebee diversity (Rundlöf et al. 2008).

Butterfly and bumblebee species richness were surprisingly high in young road verges and power line corridors. We suggest that this means that butterflies and bumblebees can colonize infrastructure habitats relatively fast, if the local conditions are suitable. All roads in the youngest age class were gravel roads and all but one were dead-end roads leading into forests. Such forest roads typically have very low traffic intensity and are managed less intensively than larger roads, both of which could have a positive effect on insect diversity (cf. Berg et al. 2011, Dániel-Ferreira et al. 2022). In addition, grassland plant richness was higher along gravel roads than along paved roads, so the resource availability was probably higher (cf. Munguira and Thomas 1992, Saarinen et al. 2005).

In contrast to our expectations, total and specialist butterfly richness in power line corridors were negatively related to the proportion of current and continuous grassland in the surrounding landscape, respectively. While several studies found positive relationships between the local butterfly diversity in semi-natural grasslands and the amount of grasslands in the surrounding landscape (Öckinger and Smith 2006, Bergman et al. 2018), studies focussing specifically on butterfly diversity in power line corridors have not found similar patterns (Berg et al. 2011, Lampinen et al. 2018, Dániel-Ferreira et al. 2023). We consider that a concentration effect of more attractive habitats is a possible explanation for the negative relationship between butterfly species richness and grassland cover in our study. Old continuous grasslands potentially contain a higher richness of specialist plants due to the long management continuity (Cousins and Eriksson 2002), and therefore specialist butterflies might have been attracted to these more suitable habitats instead of to the power line corridors, while the total butterfly richness reacted to the availability of all current grassland habitats. Regardless of the mechanism, the conclusion of this finding is that novel grasslands are particularly important butterfly habitats in landscapes where few other grasslands remain, highlighting their importance as replacement or supplementary habitat.

To address the ongoing biodiversity crisis, it has become clear that in addition to the conservation of existing valuable habitats, the restoration of degraded habitats and the appropriate management of novel and marginal habitats also have an important role to play. Our study fits well within the context of the Kunming-Montreal Global Biodiversity Framework and upcoming EU-level legislation on nature restoration. Both acknowledge the importance of urban green space, and aim on reversing pollinator declines and enabling the long-term recovery of biodiversity (Convention on Biological Diversity 2022, European Union 2022). While our study habitats are located in rural landscapes,

our results and those of similar studies emphasise their potential for biodiversity and we argue that they should be considered under the biodiversity-inclusive urban planning emphasised in the Global Biodiversity Framework. By identifying a prominence of temporal, rather than spatial factors affecting species accumulation in novel grassland habitats we highlight two conclusions of relevance for management and conservation of grassland habitats. First, management decisions should consider past habitat changes and potential time lags in the (future) establishment of local diversity (as discussed in Watts et al. 2020). Second, we show that with little grassland cover left in the landscape, the establishment of plant species in a novel habitat appears to be slow, and therefore is it of importance to conserve and restore existing valuable habitat on a landscape scale, increasing both habitat area and connectivity. Importantly, the slow assembly of plant communities can then have direct impact on pollinator diversity. Continued management of linear infrastructure habitats is therefore vital for supporting biodiversity across taxa. However, the weak or non-existent patterns for grassland specialist species highlight the importance of identifying road verges and power line corridors with local conditions that suit specialists for targeted management, while active conservation efforts such as seed sowing may be required to promote grassland biodiversity in more intensive landscapes.

*Acknowledgements* – Anna Douhan Sundahl, Carol Högfeldt, Gerard Malsher, Nina Roth, Per Haglind and Per Karlsson assisted with the field data collection and species identification.

*Funding* – This study was funded by the Swedish Research Council FORMAS (contracts 942-2015-988 and 2019-00290 to EÖ).

### Author contributions

**Svenja Horstmann:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Alistair G. Auffret:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Juliana Dániel-Ferreira:** Data curation (equal); Writing – review and editing (supporting). **Erik Öckinger:** Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06704>.

### Data availability statement

Data are available from the Swedish National Data Service: <https://doi.org/10.5878/et9j-1p32> (Horstmann et al. 2023).

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Auffret, A. G. and Lindgren, E. 2020. Roadside diversity in relation to age and surrounding source habitat: evidence for long time lags in valuable green infrastructure. – *Ecol. Solut. Evid.* 1: e12005.
- Auffret, A. G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., Wennbom, M., Wood, H., Bullock, J. M., Cousins, S. A. O., Gartz, M., Hooftman, D. A. P. and Tränk, L. 2017a. HistMapR: rapid digitization of historical land-use maps in R. – *Methods Ecol. Evol.* 8: 1453–1457.
- Auffret, A. G., Kimberley, A., Plue, J., Skånes, H., Jakobsson, S., Waldén, E., Wennbom, M., Wood, H., Bullock, J. M., Cousins, S. A. O., Gartz, M., Hooftman, D. A. P. and Tränk, L. 2017b. Data from: HistMapR: rapid digitization of historical land-use maps in R. – Stockholm Univ.
- Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pake-man, R. J., Soons, M. B., Suárez-Esteban, A., Traveset, A., Wagne-r, H. H. and Cousins, S. A. O. 2017c. Plant functional connectivity - Integrating landscape structure and effective disper-sal. – *J. Ecol.* 105: 1648–1656.
- Auffret, A. G., Kimberley, A., Plue, J. and Waldén, E. 2018. Super-regional land-use change and effects on the grassland specialist flora. – *Nat. Commun.* 9: 3464.
- Bartoń, K. 2022. MuMIn: multi-model inference. – <https://CRAN.R-project.org/package=MuMIn>.
- Berg, Å., Ahrné, K., Öckinger, E., Svensson, R. and Söderström, B. 2011. Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. – *Biol. Conserv.* 144: 2819–2831.
- Berg, Å., Bergman, K.-O., Wissman, J., Żmihorski, M. and Öckinger, E. 2016. Power-line corridors as source habitat for but-terflies in forest landscapes. – *Biol. Conserv.* 201: 320–326.
- Bergman, K.-O., Dániel-Ferreira, J., Milberg, P., Öckinger, E. and Westerberg, L. 2018. Butterflies in Swedish grasslands benefit from forest and respond to landscape composition at different spatial scales. – *Landscape Ecol.* 33: 2189–2204.
- Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Baston, D., Rouault, E., Warmerdam, F., Ooms, J. and Rundel, C. 2021a. rgdal: bindings for the “geospatial” data abstraction library. – <https://CRAN.R-project.org/package=rgdal>.
- Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K. O., Giraudoux, P., Davis, M. and Santilli, S. 2021b. rgeos: interface to geometry engine – open source (‘GEOS’). – <https://CRAN.R-project.org/package=rgeos>.
- Bommarco, R., Lindborg, R., Marini, L. and Öckinger, E. 2014. Extinction debt for plants and flower-visiting insects in landscapes with contrasting land use history. – *Divers. Distrib.* 20: 591–599.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – *R J.* 9: 378–400.
- Convention on Biological Diversity 2022. Kunming-Montreal global biodiversity framework. – <https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf>.
- Cousins, S. A. O. and Eriksson, O. 2002. The influence of man-agement history and habitat on plant species richness in a rural hemiboreal landscape, Sweden. – *Landscape Ecol.* 17: 517–529.
- Cousins, S. A. O., Auffret, A. G., Lindgren, J. and Tränk, L. 2015. Regional-scale land-cover change during the 20th century and its consequences for biodiversity. – *Ambio* 44: 17–27.
- Damschen, E. I., Brudvig, L. A., Burt, M. A., Jr, R. J. F., Haddad, N. M., Levey, D. J., Orrock, J. L., Resasco, J. and Tewksbury, J. J. 2019. Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. – *Science* 365: 1478–1480.
- Dániel-Ferreira, J., Bommarco, R., Wissman, J. and Öckinger, E. 2020. Linear infrastructure habitats increase landscape-scale diversity of plants but not of flower-visiting insects. – *Sci. Rep.* 10: 21374.
- Dániel-Ferreira, J., Berggren, Å., Bommarco, R., Wissman, J. and Öckinger, E. 2022. Bumblebee queen mortality along roads increase with traffic. – *Biol. Conserv.* 272: 109643.
- Dániel-Ferreira, J., Fourcade, Y., Bommarco, R., Wissman, J. and Öckinger, E. 2023. Communities in infrastructure habitats are species-rich but only partly support species associated with semi-natural grasslands. – *J. Appl. Ecol.*, doi: [10.1111/1365-2664.14378](https://doi.org/10.1111/1365-2664.14378).
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – *Ecography* 36: 27–46.
- Ekroos, J., Kuussaari, M., Tiainen, J., Heliölä, J., Seimola, T. and Helenius, J. 2013. Correlations in species richness between taxa depend on habitat, scale and landscape context. – *Ecol. Indic.* 34: 528–535.
- Eriksson, O. 2013. Species pools in cultural landscapes - niche construction, ecological opportunity and niche shifts. – *Ecog-raphy* 36: 403–413.
- Eriksson, O., Cousins, S. A. O. and Bruun, H. H. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. – *J. Veg. Sci.* 13: 743–748.
- European Union 2022. EU nature restoration regulation. – [https://www.europarl.europa.eu/RegData/etudes/BRIE/2022/738183/EPRS\\_BRI\(2022\)738183\\_EN.pdf](https://www.europarl.europa.eu/RegData/etudes/BRIE/2022/738183/EPRS_BRI(2022)738183_EN.pdf).
- Gardiner, M. M., Riley, C. B., Bommarco, R. and Öckinger, E. 2018. Rights-of-way: a potential conservation resource. – *Front Ecol. Environ.* 16: 149–158.
- Gustavsson, E., Lennartsson, T. and Emanuelsson, M. 2007. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. – *Biol. Conserv.* 138: 47–59.
- Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.
- Hanski, I. and Ovaskainen, O. 2002. Extinction debt at extinction threshold. – *Conserv. Biol.* 16: 666–673.
- Helsen, K., Hermy, M. and Honnay, O. 2013. Spatial isolation slows down directional plant functional group assembly in restored semi-natural grasslands. – *J. Appl. Ecol.* 50: 404–413.
- Hijmans, R. J. et al. 2022. raster: geographic data analysis and mod-eling. – <https://CRAN.R-project.org/package=raster>.
- Hill, B. and Bartomeus, I. 2016. The potential of electricity trans-mission corridors in forested areas as bumblebee habitat. – *R. Soc. Open Sci.* 3: 160525.

- Horstmann, S. 2023. Dataset: Species richness of vascular plants, butterflies and bumblebees in linear infrastructure habitats and the historical and present grassland cover in a 2 km buffer surrounding each habitat. – Swedish National Data Service, <https://doi.org/10.5878/er9j-1p32>.
- Hylander, K. and Ehrlén, J. 2013. The mechanisms causing extinction debts. – *Trends Ecol. Evol.* 28: 341–346.
- Jackson, S. T. and Sax, D. F. 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. – *Trends Ecol. Evol.* 25: 153–160.
- Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K. M., Sang, A., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter, I. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. – *Ecol. Lett.* 13: 597–605.
- 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. and Steffan-Dewenter, I. 2009. Extinction debt: a challenge for biodiversity conservation. – *Trends Ecol. Evol.* 24: 564–571.
- Lampinen, J., Ruokolainen, K. and Huhta, A.-P. 2015. Urban power line corridors as novel habitats for grassland and alien plant species in south-western Finland. – *PLoS One* 10: e0142236.
- Lampinen, J., Heikkinen, R. K., Manninen, P., Rytteri, T. and Kuussaari, M. 2018. Importance of local habitat conditions and past and present habitat connectivity for the species richness of grassland plants and butterflies in power line clearings. – *Biodivers. Conserv.* 27: 217–233.
- Lenth, R. V., Buerkner, P., Herve, M., Love, J., Miguez, F., Riebl, H. and Singmann, H. 2022. emmeans: estimated marginal means, aka least-squares means. – <https://CRAN.R-project.org/package=emmeans>.
- Lindborg, R. and Eriksson, O. 2004. Historical landscape connectivity affects present plant species diversity. – *Ecology* 85: 1840–1845.
- Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P. and Makowski, D. 2021. performance: an R package for assessment, comparison and testing of statistical models. – *J. Open Source Softw.* 6: 3139.
- Munguira, M. L. and Thomas, J. A. 1992. Use of road verges by butterfly and bumblebee populations, and the effect of roads on adult dispersal and mortality. – *J. Appl. Ecol.* 29: 316–329.
- Naturvårdsverket 2020. Nationella marktäckedata 2018 basskikt, Sverige ver. 1.1. – <https://metadatakatalogen.naturvardsverket.se/metadatakatalogen/GetMetaDataById?id=8853721d-a466-4c01-afcc-9eae57b17b39>.
- Öckinger, E. and Smith, H. G. 2006. Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. – *Oecologia* 149: 526–534.
- Öckinger, E., Lindborg, R., Sjödin, N. E. and Bommarco, R. 2012. Landscape matrix modifies richness of plants and insects in grassland fragments. – *Ecography* 35: 259–267.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P. R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E. and Wagner, H. 2020. vegan: community ecology package. – <https://CRAN.R-project.org/package=vegan>.
- Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – *Bioinformatics* 35: 526–528.
- Phillips, B. B., Wallace, C., Roberts, B. R., Whitehouse, A. T., Gaston, K. J., Bullock, J. M., Dicks, L. V. and Osborne, J. L. 2020. Enhancing road verges to aid pollinator conservation: a review. – *Biol. Conserv.* 250: 108687.
- QGIS.org 2020. QGIS geographic information system. QGIS association, ver. 3.10.12. – <http://www.qgis.org>.
- Rundlöf, M., Nilsson, H. and Smith, H. G. 2008. Interacting effects of farming practice and landscape context on bumble bees. – *Biol. Conserv.* 141: 417–426.
- Saarinen, K., Valtonen, A., Jantunen, J. and Saarnio, S. 2005. Butterflies and diurnal moths along road verges: does road type affect diversity and abundance? – *Biol. Conserv.* 123: 403–412.
- Scherreiks, P., Gossner, M. M., Ambarlı, D., Ayasse, M., Blüthgen, N., Fischer, M., Klaus, V. H., Kleinebecker, T., Neff, F., Prati, D., Seibold, S., Simons, N. K., Weisser, W. W., Wells, K., Westphal, C. and Thiele, J. 2022. Present and historical landscape structure shapes current species richness in central European grasslands. – *Landscape Ecol.* 37: 745–762.
- Steinert, M., Eldegard, K., Sydenham, M. A. K. and Moe, S. R. 2020. Bumble bee communities in power-line clearings: effects of experimental management practices. – *Insect Conserv. Divers.* 14: 377–392.
- Tischendorf, L. and Fahrig, L. 2000. On the usage and measurement of landscape connectivity. – *Oikos* 90: 7–19.
- Trakhtenbrot, A., Nathan, R., Perry, G. and Richardson, D. M. 2005. The importance of long-distance dispersal in biodiversity conservation. – *Divers. Distrib.* 11: 173–181.
- Vanneste, T. et al. 2020. Plant diversity in hedgerows and road verges across Europe. – *J. Appl. Ecol.* 57: 1244–1257.
- Watts, K., Whytock, R. C., Park, K. J., Fuentes-Montemayor, E., Macgregor, N. A., Duffield, S. and McGowan, P. J. K. 2020. Ecological time lags and the journey towards conservation success. – *Nat. Ecol. Evol.* 4: 304–311.
- Wilson, J. B., Peet, R. K., Dengler, J. and Pärtel, M. 2012. Plant species richness: the world records. – *J. Veg. Sci.* 23: 796–802.
- Wojcik, V. A. and Buchmann, S. 2012. A review of pollinator conservation and management on infrastructure supporting rights-of-way. – *J. Pollinat. Ecol.* 7.
- Zhang, D. 2021. rsq: R-squared and related measures. – <https://CRAN.R-project.org/package=rsq>.