Received: 3 July 2023 | Accepted: 3 January 2024

DOI: 10.1111/1365-2664.14592

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

# Effect of green infrastructure on restoration of pollination networks and plant performance in semi-natural dry grasslands across Europe

**Anna Traveset**[1] | **Carlos Lara-Romero**[1,2] | **Silvia Santamaría**[1] | **Gema Escribano-Ávila**[1,3] | **James M. Bullock**[4] | **Olivier Honnay**[5] | **Danny A. P. Hooftman**[4,6] | **Adam Kimberley**[7] | **Patricia Krickl**[8] | **Jan Plue**[5,7] | **Peter Poschlod**[8] | **Sara A. O. Cousins**[7]

[1]Mediterranean Institute for Advanced Studies (IMEDEA, CSIC-UIB), Esporles, Spain; [2]Research Group in Evolutionary Ecology (ECOEVO), Area of Biodiversity and Conservation, Superior School of Experimental Science and Technology (ESCET), Rey Juan Carlos University, Madrid, Spain; [3]Department of Biodiversity, Ecology and Evolution, Complutense University, Madrid, Spain; [4]UK Centre for Ecology & Hydrology, Wallingford, Oxfordshire, UK; [5]Division of Ecology, Evolution and Biodiversity Conservation, Biology Department, KU Leuven, Leuven, Belgium; [6]Lactuca, Environmental Data Analyses and Modelling, Diemen, The Netherlands; [7]Department of Physical Geography, Stockholm University, Stockholm, Sweden and [8]Ecology and Conservation Biology, Institute of Plant Sciences, University of Regensburg, Regensburg, Germany

**Correspondence**
Carlos Lara-Romero
Email: carlos.lara@urjc.es

**Funding information**
Swedish Environmental Protection Agency (Naturvårdsverket); Belgian Science Policy Office, Grant/Award Number: BELPSPO/BR/175/A1/FUNgreen; Germany Federal Ministry of Education and Research (Bundesministerium fuer Bildung und Forschung), Grant/Award Number: FKZ and 01LC1619A; Spanish Ministry of Science, Innovation and Universities (Ministerio de Ciencia, Innovación y Universidades), Grant/Award Number: PCIN-2016-077; UKCEH National Capability, Grant/Award Number: 06895; Spanish Ministry of Economy, Industry and Competitiveness (Ministerio de Economía, Industría y Competitividad) Juandela Cierva Formación postdoctoral fellowship, Grant/Award Number: FJCI-2015-24712; Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning

**Handling Editor:** Lorenzo Marini

## Abstract

1. Agricultural intensification, afforestation and land abandonment are major drivers of biodiversity loss in semi-natural grasslands across Europe. Reversing these losses requires the reinstatement of plant–animal interactions such as pollination. Here we assessed the differences in species composition and patterns of plant-pollinator interactions in ancient and restored grasslands and how these patterns are influenced by landscape connectivity, across three European regions (Belgium, Germany and Sweden).
2. We evaluated the differences in pollinator community assemblage, abundance and interaction network structure between 24 ancient and restored grasslands. We then assessed the effect of surrounding landscape functional connectivity (i.e. green infrastructure, GI) on these variables and tested possible consequences on the reproduction of two model plants, *Lotus corniculatus* and *Salvia pratensis*.
3. Neither pollinator richness nor species composition differed between ancient and restored grasslands. A high turnover of interactions across grasslands was detected but was mainly due to replacement of pollinator and plant species. The impact of grassland restoration was consistent across various pollinator functional groups, whereas the surrounding GI had differential effects. Notably, bees, butterflies, beetles, and dipterans (excluding hoverflies) exhibited the most significant responses to GI variations. Interestingly, networks in restored grasslands were more specialised (i.e. less functionally redundant) than in ancient ones and

also showed a higher number of insect visits to habitat-generalist plant species. Landscape connectivity had a similar effect, with habitat-specialist plant species receiving fewer visits at higher GI values.

4. Fruit set in *S. pratensis* and *L. corniculatus* was unaffected by grassland type or GI. However, the fruit set in the specialist *S. pratensis* increased with the number of pollinator visits, indicating a positive correlation between pollinator activity and reproductive success in this particular species.
5. *Synthesis and applications*. Our findings provide evidence of the necessity to enhance ecosystem functions while avoiding biotic homogenisation. Restoration programs should aim at increasing landscape connectivity which influences plant communities, pollinator assemblages and their interaction patterns. To avoid generalist species taking over from specialists in restored grasslands, we suggest reinforcing the presence of specialist species in the latter, for instance by means of introductions, as well as increasing the connectivity to source populations.

KEYWORDS

functional connectivity, grassland restoration, habitat quality, land-use change, plant reproductive success, plant-pollinator interactions, species richness, trophic interactions

## 1 | INTRODUCTION

European semi-natural grasslands are hotspots of biodiversity which are suffering the impacts of agricultural intensification, afforestation and abandonment (Cousins et al., 2015; Poschlod & WallisDeVries, 2002; Ridding et al., 2020). Such grasslands provide important environmental/ecosystem services, such as water supply and flow regulation, carbon storage, erosion control, climate mitigation, pollination, as well as cultural ecosystem services (Bengtsson et al., 2019; Bullock et al., 2011; Hooftman et al., 2021, 2023). The remaining fragments of ancient semi-natural grasslands are often surrounded by large areas of forest or intensively farmed, which hampers plant and animal movement among them (Auffret et al., 2015; Cousins et al., 2015; Hooftman & Bullock, 2012; Öckinger & Smith, 2007). This reduced landscape connectivity, or isolation, has shown to cause reduced population genetic diversity, lower plant species richness and smaller populations of specialist plants within remaining grasslands (Lehmair et al., 2020; Plue et al., 2022). Further effects of poorly connected landscapes may be the disruption of plant–animal interactions such as pollination networks (Clough et al., 2014; Orford et al., 2016; Rotchés-Ribalta et al., 2018).

Landscape connectivity may be determined by the amount and spatial configuration of the so-called ‘Green Infrastructure’ (GI, hereafter), defined as an ensemble of habitats such as road verges, hedgerows, grass-strips, small grassland remnants and formerly grazed forest borders, that harbour grassland species with high potential to maintain biodiversity and to supplement grassland ecosystem service provision across the landscape (modified from Hooftman et al., 2023). However, environmental conditions in these habitats are often unsuitable for maintaining viable source populations of specialised grassland plants (Dániel-Ferreira et al., 2023). Furthermore, GI habitats are likely less important as sources of food for pollinators and for their nature conservation and cultural value unless they are well-connected to ancient core grassland areas which can act as a source of unique species and genetic diversity within landscapes (Dániel-Ferreira et al., 2023; Plue et al., 2022). Indeed, increases in GI by itself appears to be insufficient to offset connectivity declines caused by the loss of semi-natural habitat, and landscape links must be functionally effective to contribute to grassland diversity (Kimberley et al., 2021).

Here, we focus on the grassland restoration effect and on the influence of landscape connectivity on one important ecosystem function, pollination and the resulting plant reproductive performance of insect-pollinated plants. Previous studies have shown that pollinator communities improve quickly after grassland restoration (reviewed in Sexton & Emery, 2020). Furthermore, pollinator traits such as mobility and resource use act as filters influencing the assemblage of pollinator communities after restoration (Öckinger & Smith, 2007). Occurrence of important pollinator functional groups like bumblebees, solitary bees, and hoverflies in the restored sites depends on such traits, such as nesting habits and migratory capacity (Öckinger & Smith, 2007). The few restoration studies that have monitored not only pollinators but plant-pollinator interactions at a community level, using a network approach, have found that networks in restored sites are significantly less complex, in terms of network connectance (fraction of all potential network links that are actually realised) and less robust (i.e. in terms of resistance to disturbances) than in ancient sites (Cusser & Goodell, 2013; Forup et al., 2008; Williams, 2011). This occurs despite plant and pollinator communities being established successfully on restored sites, and regardless of their proximity to ancient sites (Forup et al., 2008).

A lower pollinator functional redundance and lower network robustness was also reported by Williams (2011) in restored riparian communities, which showed diverse and abundant native pollinator communities but with a distinct species composition compared to the reference sites. This was attributed mainly to differences in the physical characteristics of restored sites, which may affect, for instance, nesting availability. Landscape factors such as distance from the remaining habitat patches of intact quality and areas with low floral diversity have also been reported to reduce pollinator diversity, and possibly network robustness (Cusser & Goodell, 2013). Landscape connectivity, specifically, appears to determine to a large extent which pollinators and plant-pollinator interactions can be restored. For instance, solitary bees are more likely to occur in well-connected restored grasslands whereas the opposite is found for hoverflies, although the migration capacity of the latter seems to influence their abundance in restored grasslands (Öckinger & Smith, 2007). A particular pollinator functional group may also be more species rich but less abundant in well-connected grasslands than in poorly connected (isolated) grasslands, as found by Rotchés-Ribalta et al. (2018). No effect of landscape connectivity on plant-pollinator network metrics has also been reported in at least one study (Noreika et al., 2019).

Through a large-scale study, across three European regions (Figure S1), we investigated the impacts of grassland restoration on plant-pollinator interactions and on reproductive performance of insect-pollinated plants, related to landscape connectivity. We first assessed differences in species composition and plant-pollinator interactions between ancient and restored grasslands, and then evaluated how these variables were influenced by GI. Lastly, by using a pair of plant species as model systems—*Salvia pratensis* L., representing a grassland specialist, and *Lotus corniculatus* L., embodying a grassland generalist—we examined whether and how fruit and seed set differs between both type of grasslands. Additionally, we investigated how these measures of reproductive success are modified by GI. The distinction between specialist and generalist lies in their ecological performance, with the former demonstrating a more specific habitat preference and the latter thriving across a broader range of grass types and more heterogeneous grassland environments (Grant, 1996; Moughan et al., 2021; Van Treuren et al., 1993). Specifically, we tested the following hypotheses:

1. Restored grasslands show a lower number of pollination interactions, a high interaction turnover between grasslands, and more generalised networks compared to the ancient grasslands. Due to the likely richer pollinator communities in the latter, higher reproductive success is anticipated in ancient grasslands.
2. Improved connectivity between habitats, facilitated by green infrastructure, increases both pollinator visits (abundance) and richness within grasslands, while simultaneously minimising changes in interaction patterns.
3. If Hypothesis 2 is true, this should result in higher fruit and seed set, in both grassland generalist and specialist plants. This implies that connecting habitats through green infrastructure contributes to maintain both type of species, without the necessity to reinforce the presence of specialist plants in the restored grasslands.
4. Restored grasslands with higher levels of green infrastructure closely resemble ancient grasslands in species richness, abundance, and plant-pollinator interactions due to enhanced habitat connectivity facilitating the process of plant and pollinator recolonisation.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system and sampling design

Our work is based on species surveys and digitisations of 36 landscapes across three regions in Western Europe (Hooftman et al., 2021, 2023; Kimberley et al., 2021): the Viroin valley in Belgium, the Kallmünz region in Germany, and Södermanland county and the Stockholm archipelago in Sweden (see Figure S1). In each of these three regions, 12 circular landscapes, of 1500 m radius from the centroid of a focal semi-natural grassland, were selected. Landscape area was based on the ability to generate five concentric bands of 300 m for segment selection (=1500 m) from the edge of the cores (see Hooftman et al., 2021 for detailed information). Some overlap between landscapes could not be avoided due to the low availability of such grasslands, especially in Germany (Hooftman et al., 2021). The study focused on key grasslands in various regions, each reflecting a mix of historical continuity and recent restoration efforts. Six of these grasslands had been consistently managed through grazing for centuries, while the other six were recently restored, showcasing a spectrum of contemporary structural connectivity (refer to Kimberley et al., 2021 for detailed information). Livestock, such as sheep or cattle, played a role in the grazing management of all focal grasslands. In the case of restored grasslands, restoration also included the removal of successional scrub and trees from abandoned pastures (Kimberley et al., 2021). For logistic and feasibility reasons, we did our pollinator sampling in 24 out of the 36 landscapes (see Table 1).

We considered semi-natural grassland, open forest, midfield islets, forest borders and road verges as potential 'Green Infrastructure (GI) habitats for grassland plant species' (Cousins, 2006; Lindgren et al., 2018; Poschlod & Braun-Reichert, 2017). Our estimate of landscape connectivity was the total number of hectares of GI within a 1500 m radius. This approach aligns with our overarching goal of assessing connectivity at a broad level, capturing the potential complexity and variability in landscapes with various management forms and historical conditions.

### 2.2 | Plant–pollinator interactions' survey

Plant-pollinator interactions were sampled five times at each of the 24 focal grasslands throughout the main flowering periods of 2018, shifting geographically with the flowering period (3 May–6

**TABLE 1** Network metrics and landscape information for the 24 focal semi-natural grasslands chosen to carry out the plant-pollinator interactions.

| Grassland code | Grassland type | Region | GI | Plants | Pollinators | Rarefied pollinator species richness | I | V | C | Mean # links per species | IE | $H'_2$ | $l_{wp}$ | $l_{wa}$ | Q | $Q_Z$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| B7 | Ancient | Belgium | 53.81 | 16 | 25 | 9.40 | 55 | 733 | 0.13 | 1.31 | 0.46 | 0.53 | 2.51 | 2.81 | 0.51 | 43.67 |
| B8 | Ancient | Belgium | 44.41 | 24 | 75 | 25.89 | 167 | 959 | 0.09 | 1.59 | 0.58 | 0.53 | 3.09 | 13.60 | 0.53 | 49.13 |
| B12 | Ancient | Belgium | 46.61 | 15 | 30 | 16.78 | 69 | 362 | 0.15 | 1.50 | 0.58 | 0.50 | 2.81 | 7.07 | 0.49 | 25.09 |
| B3 | Restored | Belgium | 32.80 | 17 | 34 | 19.33 | 64 | 223 | 0.11 | 1.23 | 0.56 | 0.52 | 2.16 | 7.25 | 0.47 | 17.70 |
| B4 | Restored | Belgium | 60.21 | 17 | 47 | 22.04 | 109 | 466 | 0.13 | 1.65 | 0.61 | 0.54 | 3.15 | 6.37 | 0.55 | 35.75 |
| B5 | Restored | Belgium | 35.13 | 24 | 46 | 21.04 | 120 | 550 | 0.10 | 1.67 | 0.58 | 0.54 | 3.15 | 6.04 | 0.58 | 42.25 |
| G1 | Ancient | Germany | 92.56 | 16 | 39 | 25.15 | 71 | 180 | 0.11 | 1.29 | 0.60 | 0.65 | 2.14 | 4.77 | 0.67 | 24.96 |
| G2 | Ancient | Germany | 45.60 | 17 | 41 | 22.26 | 79 | 241 | 0.11 | 1.36 | 0.59 | 0.58 | 2.46 | 5.79 | 0.53 | 21.68 |
| G3 | Ancient | Germany | 73.76 | 17 | 29 | 15.92 | 48 | 182 | 0.10 | 1.04 | 0.43 | 0.72 | 1.71 | 2.72 | 0.58 | 25.37 |
| G4 | Ancient | Germany | 95.56 | 18 | 36 | 24.40 | 60 | 154 | 0.09 | 1.11 | 0.58 | 0.67 | 1.94 | 5.02 | 0.67 | 17.14 |
| G5 | Ancient | Germany | 45.20 | 27 | 56 | 24.28 | 138 | 513 | 0.09 | 1.66 | 0.60 | 0.44 | 3.45 | 10.50 | 0.45 | 24.05 |
| G6 | Ancient | Germany | 65.57 | 23 | 38 | 21.91 | 66 | 208 | 0.08 | 1.08 | 0.54 | 0.69 | 2.01 | 3.92 | 0.63 | 24.77 |
| G8 | Restored | Germany | 78.67 | 25 | 58 | 24.06 | 112 | 391 | 0.08 | 1.35 | 0.54 | 0.66 | 2.33 | 5.35 | 0.65 | 36.65 |
| G9 | Restored | Germany | 122.04 | 27 | 39 | 23.12 | 80 | 220 | 0.08 | 1.21 | 0.55 | 0.68 | 2.32 | 3.31 | 0.71 | 29.02 |
| G10 | Restored | Germany | 104.44 | 19 | 48 | 20.11 | 100 | 526 | 0.11 | 1.49 | 0.56 | 0.60 | 2.61 | 4.86 | 0.56 | 38.73 |
| G11 | Restored | Germany | 85.61 | 13 | 49 | 25.15 | 72 | 199 | 0.11 | 1.16 | 0.58 | 0.66 | 1.98 | 6.71 | 0.61 | 18.79 |
| G12 | Restored | Germany | 52.60 | 15 | 27 | 20.08 | 56 | 163 | 0.14 | 1.33 | 0.62 | 0.62 | 2.50 | 4.50 | 0.62 | 18.24 |
| S1 | Ancient | Sweden | 101.40 | 11 | 17 | 14.29 | 26 | 81 | 0.14 | 0.93 | 0.55 | 0.50 | 2.35 | 4.82 | 0.48 | 9.31 |
| S2 | Ancient | Sweden | 80.00 | 9 | 38 | 25.22 | 52 | 134 | 0.15 | 1.11 | 0.60 | 0.67 | 1.75 | 8.84 | 0.58 | 13.99 |
| S4 | Ancient | Sweden | 120.50 | 8 | 19 | 13.63 | 30 | 124 | 0.20 | 1.11 | 0.52 | 0.42 | 2.27 | 4.40 | 0.33 | 7.65 |
| S5 | Ancient | Sweden | 98.40 | 15 | 35 | 19.86 | 63 | 206 | 0.12 | 1.26 | 0.51 | 0.58 | 2.02 | 6.50 | 0.52 | 18.31 |
| S8 | Restored | Sweden | 104.70 | 13 | 25 | 16.88 | 44 | 147 | 0.14 | 1.16 | 0.54 | 0.59 | 2.10 | 4.17 | 0.46 | 11.49 |
| S9 | Restored | Sweden | 147.50 | 10 | 22 | 22.00 | 35 | 57 | 0.16 | 1.09 | 0.60 | 0.59 | 1.90 | 4.05 | 0.64 | 7.68 |
| S10 | Restored | Sweden | 70.50 | 10 | 21 | 17.86 | 27 | 86 | 0.13 | 0.87 | 0.55 | 0.77 | 1.42 | 4.60 | 0.66 | 15.16 |

*Note*: GI is the total amount of hectares of grassland habitat within each target grassland.

Abbreviations: C, network connectance; $H'_2$, network specialisation; I, total number of different plant-pollinator interactions; IE, interaction evenness; $l_{wa}$, weighted linkage for pollinators; $l_{wp}$, weighted linkage for plants; Q, network modularity; $Q_Z$, standardised network modularity; V, total number of insect visits to flowers.

June in Germany, 14 June–8 July in Belgium and 10 July–9 August in Sweden), from 9 a.m. to 6 p.m. on sunny days with low wind, and above 15°C. Flower visitation data were gathered along three parallel linear transects (80 m long and 3 m wide) over 45 min (15 min per transect). The list of censused plants is shown in Appendix S2 and the number of plants and pollinators censused in each grassland are given in Table 1. We recorded the identity and number of insect contacts to flowers, considering only those (i.e. potential pollination events) when an insect clearly touched the flower reproductive organs. Insects were either identified in the field or collected (in Germany and Sweden) or photographed (in Belgium) for subsequent identification by expert taxonomists. Licences were not needed for fieldwork, and ethical approval was not required for the research. Sampling completeness, estimated through the Chao2 index, was rather acceptable, being 68.9% and 48.87% for pollinator richness and plant-pollinator interactions, respectively.

To facilitate the detection of general patterns, we grouped the flower visitors into 10 functional pollinator groups (set of species that tend to interact with flowers similarly; Fenster et al., 2004), namely (in alphabetical order): ants, coleopterans, dipterans (excluding hoverflies), hemipterans, hoverflies, large bees (≥1 cm), small bees (<1 cm), lepidopterans, neuropterans and wasps (see Appendix S3). Hemipterans and neuropterans were excluded from the statistical analyses (see below) as they were poorly represented in the dataset (less than 1% of visits).

## 2.3 | Plant reproductive performance

We evaluated plant reproductive success by quantifying fruit set and viable seed set of two grassland plant species that occur in all three regions: *L. corniculatus*, a common grassland generalist present in a variety of habitats (Grant, 1996; Van Treuren et al., 1993), and a more habitat specialist *S. pratensis* (Moughan et al., 2021). Both are referred hereafter as *Lotus* and *Salvia*. *Lotus* is self-incompatible, fully dependent on insect pollination to produce viable seeds (Stephenson, 1984) and pollinated by different pollinator functional groups whereas *Salvia* is self-compatible but needs pollinators to move pollen from the anther to the ovary, being mainly pollinated by bees (Van Treuren et al., 1993). At each grassland, we marked up to 10 plant individuals, if available, per species, marking all flower buds of one of the inflorescences in each individual. Before fruit dehiscence, we collected and counted the number of fruits and seeds in each. Later in the laboratory, we used an X-ray test (Bruggink, 2017) to assess seed viability, that is whether seeds contained a fully developed embryo and endosperm. The final evaluated variables were fruit set and viable seed set.

## 2.4 | Estimation of network metrics

We constructed quantitative bipartite networks using full-season data for each focal grassland, aiming to provide a comprehensive and seasonal perspective on interactions, moving beyond daily analyses. While this approach introduces the potential for 'forbidden links' due to varying flowering times, our analysis revealed no significant difference in flowering turnover between ancient and restored grasslands (ANOVA: $F_{1,18}=0.027$, $p=0.87$) or among regions (ANOVA: $F_{2,18}=2.215$, $p=0.14$). Therefore, the uniformity in flowering turnover across grassland types and regions confirms the robustness of our results. Consequently, the overall outcomes of our study are unlikely to be the result of a different probability of links between partners due to temporal mismatches.

We used visitation frequencies as a proxy for interaction strength (Vázquez et al., 2005), defining visitation frequency between pollinator *i* and plant *j* species as the total number of visits of *i* to *j*. For each grassland, we obtained the number of plant species (P) and animal species (A) and used *R* package 'bipartite' (Dormann et al., 2008) to calculate seven niche-based topological metrics that describe network performance:

(i) *total number of different plant-pollinator interactions* (I);
(ii) *total number of visits* (V);
(iii) *mean number of links/species*;
(iv) *connectance* (C = I/AP), that is the fraction of realised interactions in the network;
(v) *interaction evenness* (IE), which ranges from 0 to 1 with low values implying strong dominance in the distribution of interactions such that some links are very strong (i.e. high interaction frequencies) and many others weak;
(vi) *network specialisation* ($H'_2$), which quantifies the degree of niche divergence of elements within an entire bipartite network (Blüthgen et al., 2007) ranging from 0 (low specialisation, high niche overlap, high functional redundancy) to 1 (high specialisation, low niche overlap, low functional redundancy); and
(vii) *network modularity* (Q), which measures the extent to which species interactions are organised into modules. Q values were estimated applying Newman's modularity adapted for quantitative bipartite networks by Beckett (2016) and were corrected by comparing them to a reference distribution derived from 100 random networks constructed with the *r2dtable* algorithm (Patefield, 1981). The Q values in the randomisations were used to determine the *z*-score ($Q_Z$). This standardisation allowed us to compare the different grasslands, because Q is sensitive to network size and sampling intensity (Dormann & Strauss, 2014).

## 2.5 | Data analysis

### 2.5.1 | Pollinator species assemblages

By means of a linear model, we tested whether the type of grassland and amount of GI modified the total number of pollinator species by using rarefaction curves. Rarefied species richness for each grassland was estimated using the function 'rarefy' implemented in the R package 'vegan' (Oksanen et al., 2020), which is based on

Hurlbert's (1971) formulation. Curves were rescaled by the number of observations (i.e. number of visits) to allow for species richness comparison. All models included grassland type and region as fixed factors and amount of GI as a continuous predictor variable.

Multiple-site-β-diversity measures based on Bray–Curtis dissimilarity index were used to quantify variation in pollinator species composition between grasslands. We employed the '*betapar*' R package (Baselga et al., 2022) to compute three multiple-site beta diversity indices accounting for the: (i) balanced variation ($\beta_{BC.BAL}$, individuals of some species in one grassland are replaced by the same number of individuals of different species in another grassland) and (ii) abundance gradient components of dissimilarity ($\beta_{BC.GRA}$, whereby some individuals are lost from one grassland to the other), (iii) and the sum of both values ($\beta_{BC}$, total abundance-based dissimilarity). We then tested whether $\beta_{BC}$ was related to type of grassland, GI amount, and region using a permutational multivariate analysis of variance (PERMANOVA) on the Bray–Curtis dissimilarity matrix. The analysis was implemented in the function '*adonis 2*' in R package 'vegan' (Oksanen et al., 2020) using 999 permutations. To assess whether differences in β-diversity were due to changes in the main type of pollinator, we repeated the analyses but estimated multiple-site-β-diversity independently for each pollinator functional group.

### 2.5.2 | Network topology

Linear models were used to assess the effect of grassland type, amount of GI, and region on the different network level metrics. Grassland type and region were included as fixed factors, and amount of GI and network size (known to affect several network metrics; Blüthgen et al., 2008; Dormann & Strauss, 2014) as continuous predictor variables. Given that the mean number of links per species correlated positively with network connectance ($C$) and number of different interactions ($I$) ($r>0.5$, $p<0.001$), we used only the former as the dependent variable. The remaining selected metrics at network level (i.e. $H'_2$, IE and Q) were not significantly correlated ($r<0.2$, $p>0.5$). Finally, we fitted a linear model for the total number of visits ($V$), as it is a useful measure of the total 'volume' of the pollination function. In this model, we included the variable 'Habitat Preference' and its interaction with type of grassland and GI. Habitat preference classified the visits according to whether they were recorded on specialist grassland plant species or on generalist ones; a generalist was considered a species found in different habitats while a specialist in only one habitat (Kimberley et al., 2021). We used an identity link function with a normal distribution of residuals in all fitted linear models. Number of visits, $H'_2$, IE and $Q_Z$ were ln-transformed to reach normality and homoscedasticity.

Model residuals were checked visually for normality and homogeneity of variance using diagnostic plots (Zuur et al., 2009). The goodness-of-fit of the linear models was determined by means of the $R^2$. Linear models were fitted with the R packages 'stats' (R Core Team, 2022) and 'lme4' (Bates et al., 2015), respectively. In the case of fitted models for network metrics, where we had a sample size of 24, a model selection approach based on Akaike information criterion (AIC) was chosen. This approach is useful in the case of low statistical power, as it manages a trade-off between model fit and model complexity (Burnham & Anderson, 2002). AIC was used to evaluate full models and reduced models fitted for all variable combinations. This approach selects the 'best' model (i.e. that with the smallest AICc) and ranks the remaining models based on their AICc value. Models with AICc >4 relative to the best model were discarded, as they have less statistical support (Burnham & Anderson, 2002). We also calculated the Akaike weight ($w_i$) of each model as a proxy of model quality of adjustment (Burnham & Anderson, 2002). To quantify the relative importance of the different predictors ($w_+$) on the network metrics, we summed $w_i$ for each predictor across all the models in which it occurred; the larger this sum, the more important a given variable is relative to the other variables used in the same models (Burnham & Anderson, 2002). As there was some overlap in the circular landscapes used as replicates (as indicated in the sampling design above), Moran's tests were conducted on model residuals to assess spatial autocorrelation in the complete model. The results demonstrated no statistically significant autocorrelation (all $p>0.19$).

### 2.5.3 | Plant reproductive success

Linear models were used to evaluate whether fruit and viable seed set were affected by number of pollinator visits, grassland type, GI, region, and whether there were differences between *Lotus* and *Salvia* species. The interaction term species × grassland type was included in the models, given the different level of specialisation of the two plants. The assessment of model assumptions and goodness of fit was carried out in the same way as for the network metrics.

## 3 | RESULTS

### 3.1 | Composition of pollinator species assemblages

We recorded a total of 7105 pollinator visits across the three European regions (Appendix S3). Large bees were the most active functional group (39.8% of visits), followed by lepidopterans (21.6%), coleopterans (18.5%), hoverflies (7.14%), small bees (4.97%), dipterans—excluding hoverflies—(4.85%), wasps (1.69%) and ants (1.47%). In contrast to the expected, no overall differences in pollination richness were detected either between ancient and restored grasslands, and this was consistent across the three regions. Moreover, the amount of GI was not found to significantly influence the number of pollinator species in each target grassland ($F$-test: all $p>0.05$; Table 1; Table S1).

Regarding β diversity, there was a wide variation in the composition of pollinator assemblages across grasslands ($\beta_{BC}=0.94$), and this dissimilarity was mainly driven by spatial replacement of species

($\beta_{BC.BAL}=0.89$) rather than species loss from one grassland to another ($\beta_{BC.GRA}=0.05$). The *PERMANOVA* analyses indicated that dissimilarity in species composition was partly due to the amount of GI, as grasslands with similar GI values hosted similar pollinator assemblages (Table S2; PERMANOVA: $F_{1,19}=4.42$, $R^2=0.12$, $p<0.001$). The functional groups showing the greatest change in relation to a proportional change of GI were small bees, lepidopterans, coleopterans, large bees, and dipterans (Figure 1; Table S2). In contrast, GI did not affect the diversity of hoverflies, wasps and ants (Figure 1; Table S2: all $p>0.05$). Pollinator species composition also varied among the three regions (Table S2; PERMANOVA: $F_{1,19}=6.93$, $R^2=0.36$, $p<0.001$), which was mainly due to differences in species richness of coleopterans, large bees and small bees between them (Figure 2a). The type of grassland did not influence pollinator assemblages (Table S3; PERMANOVA: $F_{1,19}=1.13$, $R^2=0.03$, $p=0.3$), as the proportion of each pollinator functional group remained constant (Figure 2b).

## 3.2 | Changes in network topology

Region and network size were included in most of the selected models (Table 2) and therefore had the highest relative importance in explaining variation in network topology (Figure S2). GI and grassland

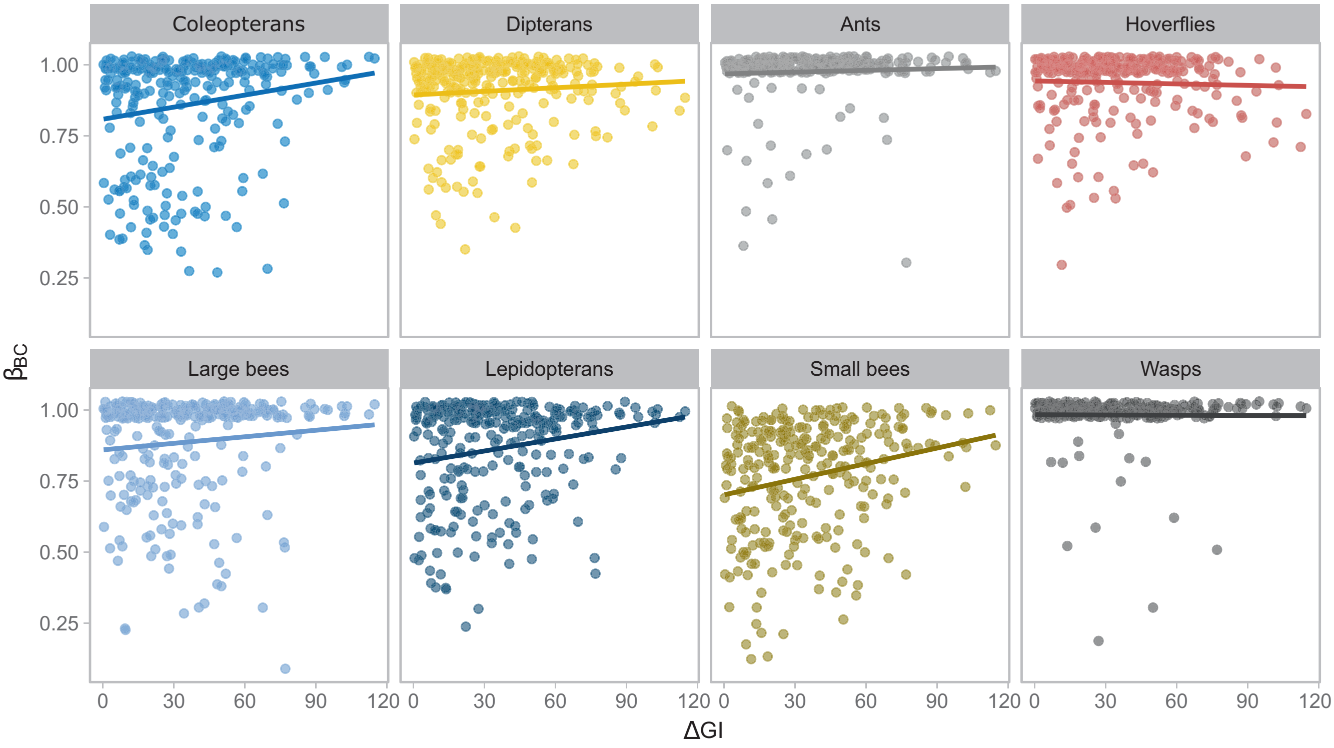


FIGURE 1 Effect of differences in the amount of green infrastructure (GI) between pairs of grasslands ($\Delta_{GI}$) on multiple site β-diversity ($\beta_{BC}$) for each pollinator functional group: coleopterans, Dipterans, ants, hoverflies, large bees, lepidopterans, small bees and wasps.

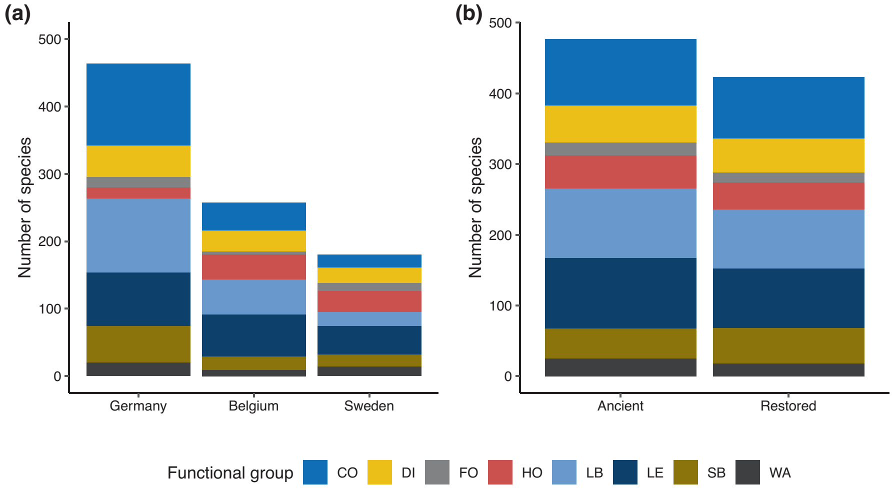


FIGURE 2 Species richness by pollinator functional group as a function of grassland type and region. Each colour represents a pollinator functional group: Coleopterans (CO), Dipterans (DI), ants (FO), hoverflies (HO), large bees (LB), lepidopterans (LE), small bees (SB) and wasps (WA). (a) Distribution of pollinator species within each functional group and region. (b) Distribution of pollinator species within each functional group and grassland type.

**TABLE 2** Best-fitting regression models for explaining network level metrics.

| | $R^2$ | df | logLik | AICc | ΔAICc | $w_i$ |
|---|---|---|---|---|---|---|
| Total number of visits | | | | | | |
| log (Visits) ~ 1 + GT + GI + HP + NS + HP:GI + HP:GT | 0.66 | 8 | −48.64 | 117.2 | — | 0.26 |
| log (Visits) ~ 1 + GT + GI + HP + NS + HP:GI | 0.64 | 7 | −50.16 | 117.3 | 0.1 | 0.25 |
| log (Visits) ~ 1 + GT + GI + HP + NS + HP:GI + HP:GT + GT:GI | 0.68 | 9 | −47.51 | 118.03 | 0.86 | 0.17 |
| log (Visits) ~ 1 + GT + GI + HP + NS + HP:GT + GT:GI | 0.65 | 8 | −49.13 | 118.16 | 0.99 | 0.16 |
| log (Visits) ~ 1 + GI + HP + NS | 0.56 | 5 | −54.54 | 120.57 | 3.40 | 0.05 |
| Interaction evenness (IE) | | | | | | |
| log (IE) ~ 1 | 0.00 | 2 | 34.38 | −64.14 | — | 0.32 |
| log (IE) ~ 1 + GI | 0.07 | 3 | 35.22 | −63.11 | 1.03 | 0.19 |
| log (IE) ~ 1 + NS | 0.02 | 3 | 34.66 | −61.98 | 2.15 | 0.11 |
| log (IE) ~ 1 + RE | 0.13 | 4 | 35.96 | −61.57 | 2.57 | 0.09 |
| log (IE) ~ 1 + GT | 0.01 | 3 | 34.44 | −61.54 | 2.59 | 0.09 |
| log (IE) ~ 1 + GT + GI | 0.08 | 4 | 35.33 | −60.30 | 3.83 | 0.05 |
| Mean # links per species | | | | | | |
| Links ~ 1 + RE + NS | 0.65 | 5 | 14.80 | −16.27 | — | 0.53 |
| Links ~ 1 + GI + NS | 0.55 | 4 | 11.73 | −13.34 | 2.92 | 0.12 |
| Links ~ 1 + NS | 0.48 | 3 | 10.01 | −12.82 | 3.45 | 0.09 |
| Links ~ 1 + RE + GT + NS | 0.65 | 6 | 14.83 | −12.72 | 3.55 | 0.09 |
| Links ~ 1 + RE + GI + NS | 0.65 | 6 | 14.81 | −12.67 | 3.60 | 0.09 |
| Network specialisation ($H'_2$) | | | | | | |
| log ($H'_2$) ~ 1 + RE | 0.29 | 4 | 17.56 | −24.90 | — | 0.28 |
| log ($H'_2$) ~ 1 + GI | 0.15 | 3 | 15.42 | −23.57 | 1.33 | 0.14 |
| log ($H'_2$) ~ 1 + RE + GT | 0.34 | 5 | 18.28 | −23.03 | 1.87 | 0.11 |
| log ($H'_2$) ~ 1 + RE + NS | 0.32 | 5 | 17.97 | −22.42 | 2.48 | 0.08 |
| log ($H'_2$) ~ 1 + RE + GI | 0.31 | 5 | 17.78 | −22.03 | 2.86 | 0.07 |
| log ($H'_2$) ~ 1 + GT + GI | 0.16 | 4 | 15.61 | −21.00 | 3.90 | 0.04 |
| Network modularity ($Q_Z$) | | | | | | |
| log ($Q_Z$) ~ 1 + RE + NS | 0.77 | 5 | −0.50 | 14.34 | — | 0.71 |
| log ($Q_Z$) ~ 1 + RE + GI | 0.77 | 6 | −0.50 | 17.94 | 3.60 | 0.12 |
| log ($Q_Z$) ~ 1 + RE + GT | 0.77 | 6 | −0.50 | 17.94 | 3.60 | 0.12 |

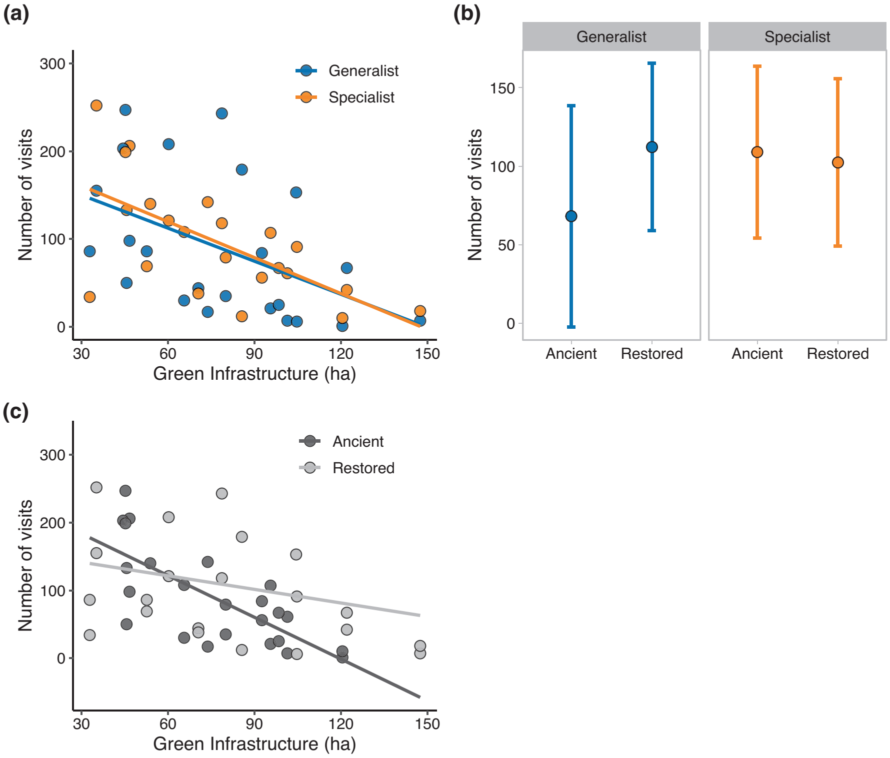
*Note*: Each row corresponds to one of the selected models in the confidence set of Delta AICc <4. Models are ranked according to the Akaike information criterion ($\text{AIC}_c$). $\text{AIC}_c$ measures the relative goodness of fit of a given model; the lower its value, the more likely this model is correct. Abbreviations: GI, green infrastructure; GT, grassland type; HP, habitat preference; NS, network size; RE, region.

type were also key factors frequently integrated into these models (Table 2; Figure S2). The models revealed that higher GI values decreased the total number of visits (Figure 3a), while restored grasslands accumulated more visits than ancient ones (Figure 3b; Table S3). The impact of GI and grassland type on visit numbers varied based on the habitat preferences of plant species (Figure 3b,c; Table 2; Table S3). Generalist plants received more visits in restored grasslands, with no significant differences for specialists (Figure 3b). The negative effect of GI on visit numbers was more pronounced for specialists than for generalist species (Table S3), and for restored than for ancient grasslands (Figure 3c; Table S3). Higher GI values led to increased network specialisation ($H'_2$) while concurrently reducing the mean number of links per species and network modularity ($Q_Z$) (Figure 4a; Table 2; Table S3). Networks were more specialised and modular in restored grasslands, while mean number of links per species also increased in restored pastures (Figures 3b; Table 2; Table S3). Grassland type and GI were also chosen by the AIC criterion to account for variation in interaction evenness, but neither of the models including GT or GI improved upon the intercept-only model (Table 2). Furthermore, their explanatory power was low ($R^2 < 0.08$ in all models).

## 3.3 | Plant reproductive success

Reproductive success was assessed for 159 *Lotus* and 42 *Salvia* individuals. *Salvia* produced more fruits per flower (0.69 ± 0.05) than *Lotus* (0.36 ± 0.03) (Table 3: $F_{1,192} = 24.86$, $p < 0.001$), but grassland

**FIGURE 3** Impact of grassland type and green infrastructure on pollinator visits to specialist and generalist grassland plants. (a) Relationship between green infrastructure (GI) and the number of pollinator visits to specialist (blue dots) and generalist (orange dots) plants in the studied grasslands. The trendline represents a linear regression for each plant group. (b) Comparison of the number of pollinator visits to specialist (blue) and generalist (orange) plants in ancient and restored grasslands. Error bars indicate standard error. (c) Relationship between GI and the number of pollinator visits to plants in ancient (dark grey) and restored (light grey) grasslands. The trendline depicts a linear regression for each plant group.



type did not affect fruit set in either species (Table 3, $p > 0.005$). Fruit set increased with the number of pollinators visits in *Salvia* but not in *Lotus* (Figure 5; Table 3: $F_{1,192} = 3.97$, $p < 0.05$). Seed viability was obtained from 123 individuals: 82 of *Lotus* and 41 of *Salvia*. Region and species were the only variables examined that had a significant effect on seed viability (Table 3; Table S3). The significant species effect was because the mean viable seed set was higher for *Lotus* than for *Salvia* ($1.64 \pm 0.41$ vs. $0.14 \pm 0.2$, respectively) (Table 3: $F_{1,93} = 5.76$, $p = 0.02$).

## 4 | DISCUSSION

Contrary to our expectations, and consistently across regions, restored and ancient grasslands did not differ in either pollinator richness or in the proportion of different pollinator functional groups. We found a high turnover of interactions across grasslands, driven by high replacement of plants and pollinators. This suggests that even though species identity may vary between ancient and restored grasslands, as well as within each grassland type, pollination functionality is maintained. Plant-pollinator interactions appear to be rapidly restored probably due to the high 'flexibility' of many pollinators allowing them to establish interactions with a wide array of plants, that is acting as generalists. This finding is concordant with previous work also reporting high responsiveness of plant pollination communities to restoration actions (e.g. Forup et al., 2008; Kaiser-Bunbury et al., 2017; Noreika et al., 2019; Tarrant et al., 2013).

Here we show that this flexibility is dependent upon landscape connectivity and that such dependence varies across pollinator functional groups. Specifically, our study provides evidence that the presence of GI in the surrounding landscape is a key factor determining pollinator species composition, especially for small and large bees, butterflies, beetles and dipterans. In contrast, GI was shown to be of minor relevance for hoverflies, wasps and ants. Differences among pollinator functional groups in responses to landscape connectivity were also documented by Öckinger and Smith (2007) and by Rotchés-Ribalta et al. (2018). In accordance with our results, the positive relationship between dissimilarity of GI and pollinator functional groups was particularly notable for bees (Rotchés-Ribalta et al., 2018) and lepidopterans (Öckinger & Smith, 2007), which can differ greatly in their effectiveness as pollinators (Ollerton, 2021).

This leads us to speculate that differing GI among grasslands may promote changes in pollinator effectiveness. The consequences of different responses by different pollinator groups for plant reproductive success and, thus, for future plant community composition, are indeed much unknown. Hence, it is important for any restoration program to consider not only total pollinator species richness but the effects on the pollinator groups that potentially have different roles in plant pollination success.

Regarding the overall structure of the plant-pollinator networks, the total number of pollinator visits as well as network specialisation varied substantially between the two grassland types. It's worth noting that the interaction between grassland type and GI was scarcely selected for nearly any model, indicating a limited effect size, which implies that the effectiveness of restoration in terms of the pollination network structure was not strongly influenced by the amount of GI. Restored grasslands received more pollinator visits than ancient ones, which indicate that they are effective at attracting pollinators, but only to generalist plant species. This led to more specialised networks, whereby pollinators

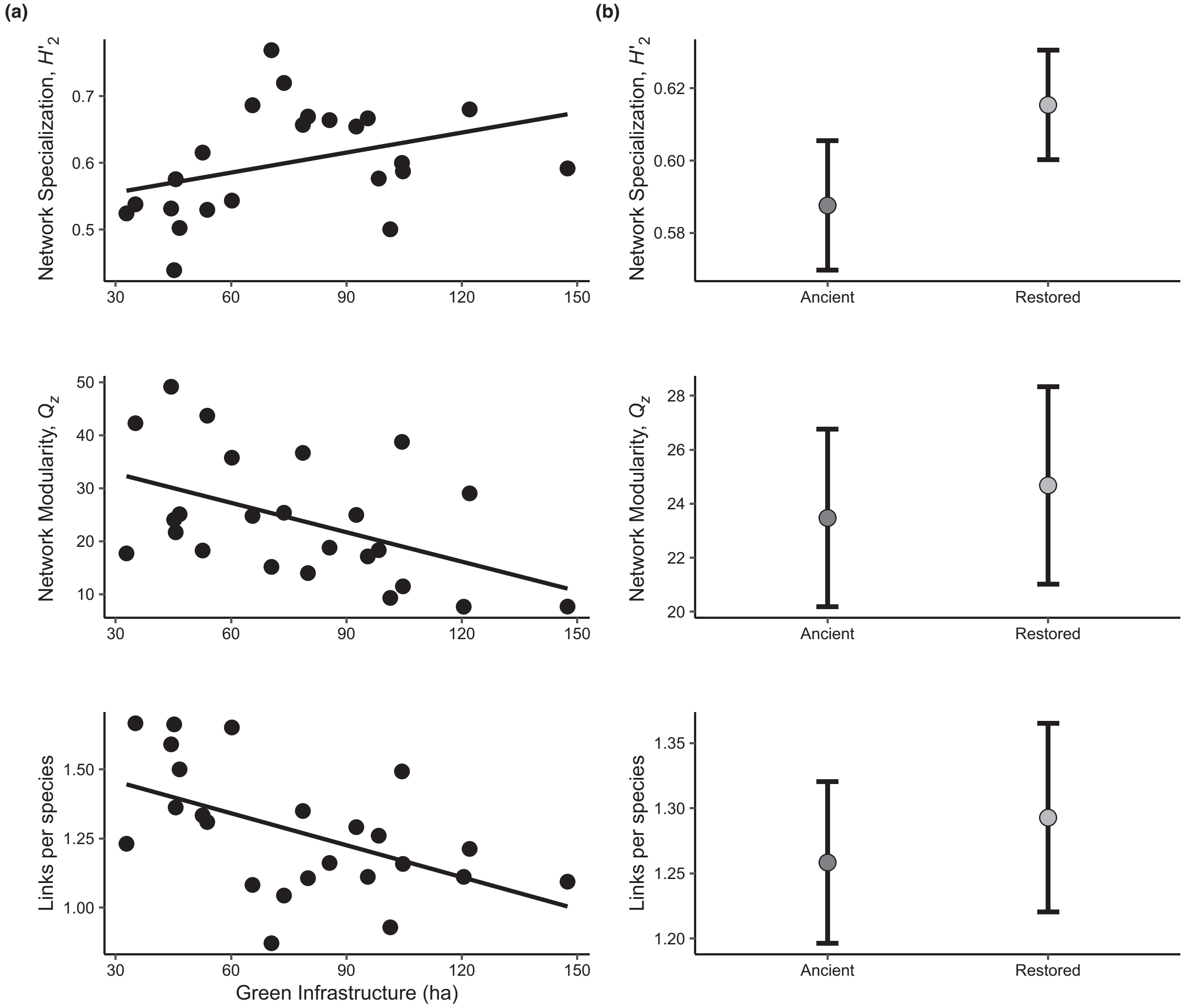


**FIGURE 4** Influence of green GI and grassland type on network metrics. (a) The impact of GI on the network-level metrics in each grassland. The trendline illustrates the fitted linear regression. (b) A comparison of network-level metrics between ancient (dark grey) and restored (light grey) grasslands. Error bars represent standard errors.

tend to be more selective and do not use resources solely on the basis of their abundance, resulting in a reduced niche overlap. This finding may imply that restored grasslands are less functionally redundant (i.e. less resilient) than their ancient counterparts, and is consistent with at least those of two previous studies who reported plant-pollinator interactions to be less robust on restored than on ancient or reference sites (Forup et al., 2008; Williams, 2011). On the other hand, the amount of GI was associated with networks exhibiting lower modularity. Specialisation and modularity often exhibit an inverse relationship as specialised pollinators tend to visit fewer plant species, leading to reduced interaction diversity and complexity, reflected in a lower mean number of links per species. Additionally, higher values of GI also correlated with a reduction in the total number of insect visits to flowers. These negative effects of landscape connectivity were stronger for grassland-specialist than for grassland-generalist plants, which is consistent with the effect of grassland type (restored vs. ancient). Interestingly, the observed increase in fruit set in the specialist *Salvia* with pollinator visits adds nuance to this narrative, hinting at potential pollination limitations in specialist species within these grasslands. Thus, restored grasslands with low amounts of GI were those promoting the highest number of insect visits to habitat-generalist plants, which might translate into higher reproductive success of generalist plant species but not specialist ones. Such findings are consistent with those of Kimberley et al. (2021) who reported that restored grasslands tend to have more generalist plant species and a lower density of grassland specialists than ancient ones, leading to biotic homogenisation.

Different restoration strategies can result into different outcomes of plant-pollination interaction network structure. This was

**TABLE 3** Effects of number of pollinator visits, grassland type (GT), region, and amount of green infrastructure (GI) on reproductive success of *Lotus corniculatus* and *Salvia pratensis*.

| Predictor | Sum of squares | df | Mean square | *F* | *p* |
|---|---|---|---|---|---|
| Fruit set | | | | | |
| Region | 1.54 | 2 | 0.77 | 6.25 | **0.002** |
| Species | 3.07 | 1 | 3.07 | 24.86 | **<0.001** |
| Pollinator visits | 0.27 | 1 | 0.27 | 2.15 | 0.144 |
| GI | 0.01 | 1 | 0.01 | 0.08 | 0.780 |
| GT | 0.08 | 1 | 0.08 | 0.66 | 0.418 |
| Species:P. visits | 0.49 | 1 | 0.49 | 3.97 | **<0.05** |
| Species:GT | 0.03 | 1 | 0.03 | 0.23 | 0.634 |
| Error | 23.72 | 192 | 0.12 | | |
| Seed set | | | | | |
| Region | 49.85 | 2 | 24.92 | 4.88 | **<0.01** |
| Species | 29.37 | 1 | 29.36 | 5.76 | **0.02** |
| Pollinator visits | 0.26 | 1 | 0.26 | 0.05 | 0.820 |
| GI | 6.88 | 1 | 6.87 | 1.34 | 0.248 |
| GT | 1.47 | 1 | 1.46 | 0.28 | 0.593 |
| Species:P. visits | 0.86 | 1 | 0.85 | 0.17 | 0.682 |
| Species:GT | 0.01 | 1 | 0.01 | 0.00 | 0.974 |
| Error | 474.11 | 93 | 5.09 | | |

*Note*: Significant effects ($p < 0.05$) are indicated in bold. Parameter estimates fitted for fixed effects are provided as Supporting Information (Table S4).

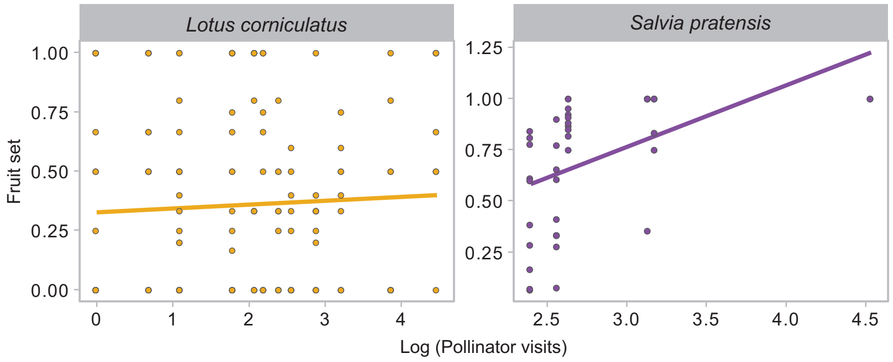


**FIGURE 5** Association between number of pollinators visits and fruit set for the two model species: *Lotus corniculatus* (left) and *Salvia pratensis* (right).

shown, by means of modelling, by Devoto et al. (2012) who found that a strategy focused on restoring functional complementarity would result into a different trajectory when compared to a strategy focused in restoring redundancy. Their findings suggest that restoration should aim at increasing both interaction diversity and evenness, properties which are typical of ancient sites. While an increase in interaction diversity can be achieved by introducing plant species, they found that interaction evenness can be enhanced by maintaining a high grassland specialist species density from the onset of the restoration. On the other hand, restoration should consider the spatial landscape configuration to improve its outcome. Our study provides new evidence that the landscape context indeed affects the interactions between plants and pollinators, not only influencing species composition and the interaction they establish, but also changing the level of generalisation of the entire pollination network, making it more or less redundant and, thus, more or less resistant to future perturbations. Network structure has been shown to be a suitable indicator for pollination quality (Kaiser-Bunbury et al., 2017) and we argue that more studies at community level, using such network approach, will help predicting how plausible different restoration programs are for these unique ecosystems. Our findings also corroborate the necessity to reconcile ecosystem functioning and species recovery to avoid biotic homogenisation. The keys to success in this aim certainly warrant further research (Holl et al., 2022). One first suggestion emerging from this study is that reinforcing the presence of specialist plants in the restored grasslands is key.

## AUTHOR CONTRIBUTIONS

Anna Traveset, Silvia Santamaría, Carlos Lara-Romero and Gema Escribano Ávila conceived the ideas and designed the methodology; Silvia Santamaría collected the plant-pollinator data at the three regions and monitored fruiting in the field, while Patricia Krickl collected the seeds in Kallmünz, S.C in Sweden and O.H. in Belgium. Carlos Lara-Romero and Gema Escribano-Ávila analysed the data; Sara Cousins, Peter Poschlod, and Olivier Honnay helped in the selection of study grasslands in Sweden, Germany and Belgium, respectively. Adam Kimberley, James M. Bullock, Jan Plue and Danny A. P. Hooftman were heavily involved in project design both in the acquisition phase and practically. Anna Traveset and Carlos Lara-Romero led the writing of the manuscript with important contributions from Gema Escribano-Ávila and Silvia Santamaría.

## ACKNOWLEDGEMENTS

This research was funded through the 2015–2016 BiodivERsA COFUND call for research proposals, with the national funders FORMAS (2016–01948), the Swedish Environmental Protection Agency (Naturvårdsverket), the Belgian Science Policy Office (BelSPo, BELPSPO/BR/175/A1/FUNgreen), the Germany Federal Ministry of Education and Research (Bundesministerium fuer Bildung und Forschung, FKZ: 01LC1619A) and the Spanish Ministry of Science, Innovation and Universities (Ministerio de Ciencia, Innovación y Universidades, PCIN-2016-077). JMB was funded under UKCEH National Capability project 06895; DAPH was contracted from Stockholm University as external scientist (contract reference 463). CLR was supported by a Juan de la Cierva Formación postdoctoral fellowship (Ministerio de Economía, Industria y Competitividad: FJCI-2015-24712). We are very grateful to all landowners that allowed us to work in their fields. We thank Alberto García Calvente and Daniel Lenz for their field work in Belgium and Germany, respectively; and Juan Carlos Alonso and Araceli Guillem for seed processing. We also acknowledge the valuable work done by Óscar Luis Aguado, Santiago Bordera Sanjuán, Xavier Canyelles, Miguel Carles-Tolrá, Carl-Cedric Coulianos, Leopoldo Castro, Xavier Espalader, Vicent Falcó, Miguel Ángel González Estévez, Patrick Grootaert, Bert Gustafsson, Mattias Jentzsch, Emilia Narchuk, Nick Owens, Thomas Pape, Marc Pollet, Adrian Pont, Carmen Rey del Castillo, Chris Saure, Axel Ssymank, Hanspeter Tschorsnig, Jeroen van Steenis and Daniel Ventura who identified insects. Plant inventories in each of these countries were performed by Maria Björk, Kasper van Acker, Robbe Cool and Lotje Vanhove, respectively. Maxi Bleicher and Irina Weinberger (Ecology and Conservation Biology, Institue of Plant Sciences, University of Regensburg) did the seed viability tests.

## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.fbg79cp2t (Lara-Romero et al., 2024).

## STATEMENT ON INCLUSION

All authors contributed critically to the drafts and gave final approval for publication. Our study brings together authors from several different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited.

## ORCID

*Anna Traveset* https://orcid.org/0000-0002-1816-1334
*Carlos Lara-Romero* https://orcid.org/0000-0003-0962-0567
*Gema Escribano-Ávila* https://orcid.org/0000-0003-1362-8924
*James M. Bullock* https://orcid.org/0000-0003-0529-4020
*Danny A. P. Hooftman* https://orcid.org/0000-0001-9835-6897
*Adam Kimberley* https://orcid.org/0000-0002-0807-9943
*Jan Plue* https://orcid.org/0000-0002-6999-669X
*Peter Poschlod* https://orcid.org/0000-0003-4473-7656
*Sara A. O. Cousins* https://orcid.org/0000-0003-2656-2645

## REFERENCES

Auffret, A. G., Plue, J., & Cousins, S. A. O. (2015). The spatial and temporal components of functional connectivity in fragmented landscapes. *Ambio*, *44*, S51–S59. https://doi.org/10.1007/s13280-014-0588-6

Baselga, A., Gomez-Rodriguez, C., Araujo, M. B., Castro-Insua, A., Arenas, M., Posada, D., & Vogler, A. P. (2022). Joint analysis of species and genetic variation to quantify the role of dispersal and environmental constraints in community turnover. *Ecography*, *5*, e05808. https://doi.org/10.1111/ecog.05808

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

Beckett, S. J. (2016). Improved community detection in weighted bipartite networks. *Royal Society Open Science*, *3*, 140536. https://doi.org/10.1098/rsos.140536

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*, e02582. https://doi.org/10.1002/ecs2.2582

Blüthgen, N., Frund, J., Vazquez, D. P., & Menzel, F. (2008). What do interaction network metrics tell us about specialization and biological traits? *Ecology*, *89*, 3387–3399. https://doi.org/10.1890/07-2121.1

Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N. (2007). Specialization, constraints, and conflicting interests in mutualistic networks. *Current Biology*, *17*, 341–346. https://doi.org/10.1016/j.cub.2006.12.039

Bruggink, H. (2017). *X-ray based seed analysis and sorting*. Paper presented at ISTA conference.

Bullock, J. M., Aronson, J., Newton, A. C., Pywell, R. F., & Rey-Benayas, J. M. (2011). Restoration of ecosystem services and biodiversity: Conflicts and opportunities. *Trends in Ecology & Evolution*, *26*, 541–549. https://doi.org/10.1016/j.tree.2011.06.011

Burnham, K. P., & Anderson, D. R. (2002). Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, *28*, 111–119. https://doi.org/10.1071/WR99107

Clough, Y., Ekroos, J., Báldi, A., Batáry, P., Bommarco, R., Gross, N., Holzschuh, A., Hopfenmüller, S., Knop, E., Kuussaari, M., Lindborg, R., Marini, L., Öckinger, E., Potts, S. G., Pöyry, J., Roberts, S. P., Steffan-Dewenter, I., & Smith, H. G. (2014). Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters*, *17*, 1168–1177. https://doi.org/10.1111/ele.12325

Cousins, S. A. O. (2006). Plant species richness in midfield islets and road verges–the effect of landscape fragmentation. *Biological Conservation*, *127*, 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*, 17–27. https://doi.org/10.1007/s13280-014-0585-9

Cusser, S., & Goodell, K. (2013). Diversity and distribution of floral resources influence the restoration of plant–pollinator networks on a reclaimed strip mine. *Restoration Ecology*, *21*, 713–721. https://doi.org/10.1111/rec.12003

Dániel-Ferreira, J., Fourcade, Y., Bommarco, R., Wissman, J., & Öckinger, E. (2023). Communities in infrastructure habitats are species rich but only partly support species associated with semi-natural grasslands. *Journal of Applied Ecology*, *60*, 837–848. https://doi.org/10.1111/1365-2664.14378

Devoto, M., Bailey, S., Craze, P., & Memmott, J. (2012). Understanding and planning ecological restoration of plant–pollinator networks. *Ecology Letters*, *15*, 319–328. https://doi.org/10.1111/j.1461-0248.2012.01740.x

Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analysing ecological networks. *Interaction*, *1*(0.2413793), 8–11.

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, *5*, 90–98. https://doi.org/10.1111/2041-210X.12139

Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

Forup, M. L., Henson, K. S. E., Craze, P. G., & Memmott, J. (2008). The restoration of ecological interactions: Plant-pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology*, *45*, 742–752. https://doi.org/10.1111/j.1365-2664.2007.01390.x

Grant, W. F. (1996). Seed pod shattering in the genus *Lotus* (Fabaceae): A synthesis of diverse evidence. *Canadian Journal of Plant Science*, *76*(3), 447–456. https://doi.org/10.4141/cjps96-079

Holl, K. D., Luong, J. C., & Brancalion, P. H. (2022). Overcoming biotic homogenization in ecological restoration. *Trends in Ecology & Evolution*, *37*, 777–788. https://doi.org/10.1016/j.tree.2022.05.002

Hooftman, D. A. P., & Bullock, J. M. (2012). Mapping to inform conservation: A case study of changes in semi-natural habitats and their connectivity over 70 years. *Biological Conservation*, *145*, 30–38. https://doi.org/10.1016/j.biocon.2011.09.015

Hooftman, D. A. P., 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

Hooftman, D. A. P., Kimberley, A., Cousins, S. A. O., Santamaría, S., Honnay, O., Krickl, P., Plue, J., Poschlod, P., Traveset, A., & Bullock, J. M. (2023). Could green infrastructure supplement ecosystem service provision from semi-natural grasslands? *Journal of Environmental Management*, *328*, 116952. https://doi.org/10.1016/j.jenvman.2022.116952

Hurlbert, S. H. (1971). Nonconcept of species diversity—Critique and alternative parameters. *Ecology*, *52*, 577–586. https://doi.org/10.2307/1934145

Kaiser-Bunbury, C., Mougal, J., Whittington, A. E., Valentin, T., Gabriel, R., Olesen, J. M., & Bluthgen, N. (2017). Ecosystem restoration strengthens pollination network resilience and function. *Nature*, *542*, 223–227. https://doi.org/10.1038/nature21071

Kimberley, A., Hooftman, D. A. P., 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*, 265–280. https://doi.org/10.1007/s10980-020-01138-x

Lara-Romero, C., Traveset, A., Santamaría, S., Escribano-Ávila, G., Bullock, J. M., Honnay, O., Hooftman, D. A. P., Kimberley, A., Crickl, P., Plue, J., Poschlod, P., & Cousins, S. A. O. (2024). Data from: Effect of green infrastructure on restoration of pollination networks and plant performance in semi-natural dry grasslands across Europe. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.fbg79cp2t

Lehmair, T. A., Pagel, E., Poschlod, P., & Reisch, C. (2020). Surrounding landscape structures, rather than habitat age, drive genetic variation of typical calcareous grassland plant species. *Landscape Ecology*, *35*, 2881–2893.

Lindgren, J., Lindborg, R., & Cousins, S. A. O. (2018). Local conditions in small habitats and surrounding landscape are important for pollination services, biological pest control and seed predation. *Agriculture, Ecosystems & Environment*, *251*, 107–113. https://doi.org/10.1016/j.agee.2017.09.025

Moughan, J., McGinn, K. J., Jones, L., Rich, T. C., Waters, E., & de Vere, N. (2021). Biological Flora of the British Isles: *Salvia pratensis*. *Journal of Ecology*, *109*(12), 4171–4190. https://doi.org/10.1111/1365-2745.13805

Noreika, N., Bartomeus, I., Winsa, M., Bommarco, R., & Ockinger, E. (2019). Pollinator foraging flexibility mediates rapid plant-pollinator network restoration in semi-natural grasslands. *Scientific Reports*, *9*, 15473. https://doi.org/10.1038/s41598-019-51912-4

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

Oksanen, J., Blanchet, F. 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. https://cran.r-project.org/package=vegan

Ollerton, J. (2021). *Pollinators & pollination. Nature and society*. Pelagic Publishing.

Orford, K. A., Murray, P. J., Vaughan, I. P., & Memmott, J. (2016). Modest enhancements to conventional grassland diversity improve the provision of pollination services. *Journal of Applied Ecology*, *53*, 906–915. https://doi.org/10.1111/1365-2664.12608

Patefield, W. M. (1981). Multivariate linear relationships—Maximum-likelihood estimation and regression bounds. *Journal of the Royal Statistical Society, Series B: Methodological*, *43*, 342–352.

Plue, J., Kimberley, A., Bullock, J. M., Hellemans, B., Hooftman, D. A. P., Krickl, P., Leus, L., Peeters, G., Poschlod, P., Traveset, A., Volckaert, F., Cousins, S. A. O., & Honnay, O. (2022). Green infrastructure can promote plant functional connectivity in a grassland species around fragmented semi-natural grasslands in NW-Europe. *Ecography*, *2022*, e06290. https://doi.org/10.1111/ecog.06290

Poschlod, P., & Braun-Reichert, R. (2017). Small natural features with large ecological roles in ancient agricultural landscapes of Central Europe - history, value, status, and conservation. *Biological Conservation*, *211*, 60–68. https://doi.org/10.1016/j.biocon.2016.12.016

Poschlod, P., & WallisDeVries, M. F. (2002). The historical and socioeconomic perspective of calcareous grasslands–lessons from the distant and recent past. *Biological Conservation*, *104*, 361–376. https://doi.org/10.1016/S0006-3207(01)00191-4

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ridding, L. E., Watson, S. C. L., Newton, A. C., Rowland, C. S., & Bullock, J. M. (2020). Ongoing, but slowing, habitat loss in a rural landscape over 85 years. *Landscape Ecology*, *35*, 257–273. https://doi.org/10.1007/s10980-019-00944-2

Rotchés-Ribalta, R., Winsa, M., Roberts, S. P. M., & Öckinger, E. (2018). Associations between plant and pollinator communities under grassland restoration respond mainly to landscape connectivity.

*Journal of Applied Ecology*, *55*, 2822–2833. https://doi.org/10.1111/1365-2664.13232

Sexton, A. N., & Emery, S. M. (2020). Grassland restorations improve pollinator communities: A meta-analysis. *Journal of Insect Conservation*, *24*, 719–726. https://doi.org/10.1007/s10841-020-00247-x

Stephenson, A. G. (1984). The regulation of maternal investment in an indeterminate flowering plant (*Lotus corniculatus*). *Ecology*, *65*, 113–121. https://doi.org/10.2307/1939464

Tarrant, S., Ollerton, J., Rahman, M. L., Tarrant, J., & McCollin, D. (2013). Grassland restoration on landfill sites in the east midlands, United Kingdom: An evaluation of floral resources and pollinating insects. *Restoration Ecology*, *21*, 560–568. https://doi.org/10.1111/j.1526-100X.2012.00942.x

Van Treuren, R., Bijlsma, R., Ouborg, N. J., & Vandelden, W. (1993). The effects of population size and plant density on outcrossing rates in locally endangered *Salvia pratensis*. *Evolution*, *47*, 1094–1104. https://doi.org/10.1111/j.1558-5646.1993.tb02138.x

Vázquez, D. P., Poulin, R., Krasnov, B. R., & Shenbrot, G. I. (2005). Species abundance and the distribution of specialization in host–parasite interaction networks. *Journal of Animal Ecology*, *74*, 946–955. https://doi.org/10.1111/j.1365-2656.2005.00992.x

Williams, N. M. (2011). Restoration of nontarget species: Bee communities and pollination function in riparian forest. *Restoration Ecology*, *19*, 450–459. https://doi.org/10.1111/j.1526-100X.2010.00707.x

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2009). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1:** Tables and figures for in-depth information.

**Appendix S2:** Plant species visited by insects during pollination surveys in the three regions: Germany (G), Belgium (B) and/or Sweden (S).

**Appendix S3:** Pollinator species recorded during pollination surveys in the three regions: Germany (G), Belgium (B) and/or Sweden (S).

**How to cite this article:** Traveset, A., Lara-Romero, C., Santamaría, S., Escribano-Ávila, G., Bullock, J. M., Honnay, O., Hooftman, D. A. P., Kimberley, A., Krickl, P., Plue, J., Poschlod, P., & Cousins, S. A. O. (2024). Effect of green infrastructure on restoration of pollination networks and plant performance in semi-natural dry grasslands across Europe. *Journal of Applied Ecology*, *61*, 1015–1028. https://doi.org/10.1111/1365-2664.14592