

1 **Effect of green infrastructure on restoration of pollination**
2 **networks and plant performance in semi-natural dry grasslands across Europe**
3

4 **Anna Traveset¹, Carlos Lara-Romero^{1,2*}, Silvia Santamaría¹, Gema Escribano-Ávila^{1,3}, James M.**
5 **Bullock⁴, Olivier Honnay⁵, Danny A.P. Hooftman^{4,6}, Adam Kimberley⁷, Patricia Krickl⁸, Jan Plue^{5,7},**
6 **Peter Poschlod⁸, and Sara A.O. Cousins⁷**

7 ¹Mediterranean Institute for Advanced Studies (IMEDEA, UIB-CSIC), Esporles, Spain

8 ²Research Group in Evolutionary Ecology (ECOevo), Area of Biodiversity and Conservation, Superior School of
9 Experimental Science and Technology (ESCET), Rey Juan Carlos University, Madrid, Spain

10 ³ Department of Biodiversity, Ecology and Evolution, Complutense University. C/ José Antonio Novais 12, Ciudad
11 Universitaria, 28040 Madrid. Spain

12 ⁴ UK Centre for Ecology & Hydrology, OX10 8BB, Wallingford, Oxfordshire, UK

13 ⁵ Division of Ecology, Evolution and Biodiversity Conservation, Biology Department, KU Leuven, Kasteelpark
14 Arenberg 31, 3001, Leuven, Belgium

15 ⁶ Lactuca, Environmental Data Analyses and Modelling, Diemen, 1112NC, The Netherlands

16 ⁷ Department of Physical Geography, Stockholm University, SE-106 91, Stockholm, Sweden

17 ⁸ Ecology and Conservation Biology, Institute of Plant Sciences, University of Regensburg, Universitaetsstrasse 31, D-
18 93053, Regensburg, Germany

19 *Corresponding author: carlos.lara@urjc.es
20

21 **ABSTRACT**

- 22 1. Agricultural intensification, afforestation and land abandonment are major drivers of biodiversity loss
23 in semi-natural grasslands across Europe. Reversing these losses requires the reinstatement of plant-
24 animal interactions such as pollination. Here we assessed the differences in species composition and
25 patterns of plant-pollinator interactions in ancient and restored grasslands and how these patterns are
26 influenced by landscape connectivity, across three European regions (Belgium, Germany and
27 Sweden).
- 28 2. We evaluated the differences in pollinator community assemblage, abundance, and interaction network
29 structure between 24 ancient and restored grasslands. We then assessed the effect of surrounding
30 landscape functional connectivity (i.e. green infrastructure, GI) on these variables and tested possible
31 consequences on the reproduction of two model plants, *Lotus corniculatus* and *Salvia pratensis*.
- 32 3. Neither pollinator richness nor species composition differed between ancient and restored grasslands.
33 A high turnover of interactions across grasslands was detected but was mainly due to replacement of
34 pollinator and plant species. The impact of grassland restoration was consistent across various
35 pollinator functional groups, whereas the surrounding GI had differential effects. Notably, bees,
36 butterflies, beetles, and dipterans (excluding hoverflies) exhibited the most significant responses to GI
37 variations. Interestingly, networks in restored grasslands were more specialised (i.e. less functionally
38 redundant) than in ancient ones and also showed a higher number of insect visits to habitat-generalist
39 plant species. Landscape connectivity had a similar effect, with habitat-specialist plant species
40 receiving fewer visits at higher GI values.
- 41 4. Fruit set in *S. pratensis* and *L. corniculatus* was unaffected by grassland type or GI. However, the fruit
42 set in the specialist *S. pratensis* increased with the number of pollinator visits, indicating a positive
43 correlation between pollinator activity and reproductive success in this particular species..
- 44 5. *Synthesis and applications.* Our findings provide evidence of the necessity to enhance ecosystem
45 functions while avoiding biotic homogenization. Restoration programs should aim at increasing
46 landscape connectivity which influences plant communities, pollinator assemblages, and their
47 interaction patterns. To avoid generalist species taking over from specialists in restored grasslands, we

48 suggest reinforcing the presence of specialist species in the latter, for instance by means of
49 introductions, as well as increasing the connectivity to source populations.

50

51 **KEYWORDS**

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

54 **NON-ENGLISH ABSTRACT**

55 1. La intensificación agrícola, la forestación y el abandono de tierras son factores clave en la pérdida de
56 biodiversidad en pastizales semi-naturales en toda Europa. Revertir estas pérdidas requiere restablecer
57 interacciones planta-animal, como la polinización. En este estudio, evaluamos las diferencias en la
58 composición de especies y patrones de interacciones planta-polinizador en pastizales antiguos y
59 restaurados, y cómo estos patrones son influenciados por la conectividad del paisaje en tres regiones
60 europeas (Bélgica, Alemania y Suecia).

61 2. Examinamos las diferencias en el ensamblaje de la comunidad de polinizadores, su abundancia y la
62 estructura de la red de interacciones planta-polinizador en 24 pastizales antiguos y restaurados. Luego,
63 evaluamos el efecto de la conectividad funcional del paisaje circundante (es decir, infraestructura
64 verde, GI) en estas variables y evaluamos posibles consecuencias en la reproducción de dos plantas
65 modelo, *Lotus corniculatus* y *Salvia pratensis*.

66 3. No hubo diferencias en la riqueza de polinizadores ni en la composición de especies entre los pastizales
67 antiguos y restaurados. El impacto de la restauración de pastizales fue consistente en diversos grupos
68 funcionales de polinizadores, mientras que la GI circundante tuvo efectos diferenciales.
69 Destacadamente, abejas, mariposas, escarabajos y dípteros (excluyendo sírfidos) mostraron las
70 respuestas más significativas a las variaciones en la GI. Curiosamente, las redes en pastizales
71 restaurados fueron más especializadas (menos funcionalmente redundantes) que en los antiguos y
72 también mostraron un mayor número de visitas de insectos a especies de plantas generalistas de
73 hábitat. La conectividad del paisaje tuvo un efecto similar, con especies de plantas especializadas
74 recibiendo menos visitas a mayores valores de GI.

75 4. La producción de frutos en *S. pratensis* y *L. corniculatus* no se vió afectada por el tipo de pastizal o la
76 GI. Sin embargo, la producción de frutos en la especialista *S. pratensis* aumentó con el número de

77 visitas de polinizadores, indicando una correlación positiva entre la actividad de polinización y el éxito
78 reproductivo en esta especie.

79 5. Síntesis y aplicaciones. Nuestros resultados evidencian la necesidad de evitar la homogeneización
80 biótica. Los programas de restauración deben apuntar a aumentar la conectividad del paisaje, que
81 influye en las comunidades de plantas y polinizadores y sus patrones de interacción. Para evitar que
82 especies generalistas desplacen a especialistas en pastizales restaurados, sugerimos reforzar la
83 presencia de especies especialistas en estos, por ejemplo, mediante introducciones, así como aumentar
84 la conectividad con poblaciones fuente.

85

86 1 INTRODUCTION

87 European semi-natural grasslands are hotspots of biodiversity which are suffering the impacts of
88 agricultural intensification, afforestation and abandonment (Poschlod & WallisDeVries, 2002; Cousins et al.,
89 2015; Ridding et al., 2020). Such grasslands provide important environmental/ecosystem services, such as
90 water supply and flow regulation, carbon storage, erosion control, climate mitigation, pollination, as well as
91 cultural ecosystem services (Bullock et al., 2011; Bengtsson et al., 2019; Hooftman et al., 2021, 2023). The
92 remaining fragments of ancient semi-natural grasslands are often surrounded by large areas of forest or
93 intensively farmed, which hampers plant and animal movement among them (Hooftman & Bullock, 2012;
94 Auffret et al., 2015; Cousins et al., 2015; Öckinger et al., 2017). This reduced landscape connectivity, or
95 isolation, has shown to cause reduced population genetic diversity, lower plant species richness, and smaller
96 populations of specialist plants within remaining grasslands (Lehmair et al., 2020; Plue et al., 2022). Further
97 effects of poorly connected landscapes may be the disruption of plant-animal interactions such as pollination
98 networks (Clough et al., 2014; Orford et al., 2016; Rotchés-Ribalta et al., 2018).

99 Landscape connectivity may be determined by the amount and spatial configuration of the so-called
100 ‘Green Infrastructure’ (GI, hereafter), defined as an ensemble of habitats such as road verges, hedgerows,
101 grass-strips, small grassland remnants and formerly grazed forest borders, that harbour grassland species with
102 high potential to maintain biodiversity and to supplement grassland ecosystem service provision across the
103 landscape (modified from Hooftman et al., 2023). However, environmental conditions in these habitats are
104 often unsuitable for maintaining viable source populations of specialised grassland plants (Dániel-Ferreira et

105 al., 2023). Furthermore, GI habitats are likely less important as sources of food for pollinators and for their
106 nature conservation and cultural value unless they are well-connected to ancient core grassland areas which
107 can act as a source of unique species and genetic diversity within landscapes (Plue et al., 2022, Dániel-Ferreira
108 et al. 2023). Indeed, increases in GI by itself appears to be insufficient to offset connectivity declines caused
109 by the loss of semi-natural habitat, and landscape links must be functionally effective to contribute to grassland
110 diversity (Kimberley et al., 2021).

111 Here, we focus on the grassland restoration effect and on the influence of landscape connectivity on
112 one important ecosystem function, pollination and the resulting plant reproductive performance of insect-
113 pollinated plants. Previous studies have shown that pollinator communities improve quickly after grassland
114 restoration (reviewed in Sexton & Emery, 2020). Furthermore, pollinator traits such as mobility and resource
115 use act as filters influencing the assemblage of pollinator communities after restoration (Öckinger et al., 2017).
116 Occurrence of important pollinator functional groups like bumblebees, solitary bees, and hoverflies in the
117 restored sites depends on such traits, such as nesting habits and migratory capacity (Öckinger et al., 2017). The
118 few restoration studies that have monitored not only pollinators but plant-pollinator interactions at a
119 community level, using a network approach, have found that networks in restored sites are significantly less
120 complex, in terms of network connectance (fraction of all potential network links that are actually realized)
121 and less robust (i.e. in terms of resistance to disturbances) than in ancient sites (Forup et al., 2008; Williams
122 2011; Cusser and Goodell, 2013). This occurs despite plant and pollinator communities being established
123 successfully on restored sites, and regardless of their proximity to ancient sites (Forup et al., 2008). A lower
124 pollinator functional redundance and lower network robustness was also reported by Williams (2011) in
125 restored riparian communities, which showed diverse and abundant native pollinator communities but with a
126 distinct species composition compared to the reference sites. This was attributed mainly to differences in the
127 physical characteristics of restored sites, which may affect, for instance, nesting availability. Landscape factors
128 such as distance from the remaining habitat patches of intact quality and areas with low floral diversity have
129 also been reported to reduce pollinator diversity, and possibly network robustness (Cusser & Goodell, 2013).
130 Landscape connectivity, specifically, appears to determine to a large extent which pollinators and plant-
131 pollinator interactions can be restored. For instance, solitary bees are more likely to occur in well-connected
132 restored grasslands whereas the opposite is found for hoverflies, although the migration capacity of the latter

133 seems to influence their abundance in restored grasslands (Öckinger et al., 2017). A particular pollinator
134 functional group may also be more species rich but less abundant in well-connected grasslands than in poorly
135 connected (isolated) grasslands, as found by Rotchés-Ribalta et al. (2018). No effect of landscape connectivity
136 on plant-pollinator network metrics has also been reported in at least one study (Noreika et al., 2019).

137 Through a large-scale study, across three European regions (Fig. 1S), we investigated the impacts of
138 grassland restoration on plant-pollinator interactions and on reproductive performance of insect-pollinated
139 plants, related to landscape connectivity. We first assessed differences in species composition and plant-
140 pollinator interactions between ancient and restored grasslands, and then evaluated how these variables were
141 influenced by GI. Lastly, by using a pair of plant species as model systems -*Salvia pratensis* L., representing
142 a grassland specialist, and *Lotus corniculatus* L., embodying a grassland generalist- we examined whether and
143 how fruit and seed set differs between both type of grasslands. Additionally, we investigated how these
144 measures of reproductive success are modified by GI. The distinction between specialist and generalist lies in
145 their ecological performance, with the former demonstrating a more specific habitat preference and the latter
146 thriving across a broader range of grass types and more heterogeneous grassland environments (Moughan et
147 al., 2021; van Treuren et al., 1993, Grant 1996). Specifically, we tested the following hypotheses:

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

160 **2. MATERIALS AND METHODS**

161 **2.1 Study system and sampling design**

162 Our work is based on species surveys and digitisations of 36 landscapes across three regions in Western
163 Europe (Hooftman et al., 2021, 2023; Kimberley et al., 2021): the Viroin valley in Belgium, the Kallmünz
164 region in Germany, and Södermanland county and the Stockholm archipelago in Sweden (see Figure S1 in
165 Appendix S1 within the Supporting Information). In each of these three regions, 12 circular landscapes, of
166 1500 m radius from the centroid of a focal semi-natural grassland, were selected. Landscape area was based
167 on the ability to generate five concentric bands of 300 meters for segment selection (=1500m) from the edge
168 of the cores (see Hooftman et al., 2021 for detailed information). Some overlap between landscapes could not
169 be avoided due to the low availability of such grasslands, especially in Germany (Hooftman et al., 2021). The
170 study focused on key grasslands in various regions, each reflecting a mix of historical continuity and recent
171 restoration efforts. Six of these grasslands had been consistently managed through grazing for centuries, while
172 the other six were recently restored, showcasing a spectrum of contemporary structural connectivity (refer to
173 Kimberley et al., 2021 for detailed information). Livestock, such as sheep or cattle, played a role in the grazing
174 management of all focal grasslands. In the case of restored grasslands, restoration also included the removal
175 of successional scrub and trees from abandoned pastures (Kimberley et al., 2021). For logistic and feasibility
176 reasons, we did our pollinator sampling in 24 out of the 36 landscapes (see Table 1).

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

183 **2.2. Plant–pollinator interactions’ survey**

184 Plant-pollinator interactions were sampled five times at each of the 24 focal grasslands throughout the
185 main flowering periods of 2018, shifting geographically with the flowering period (May 3rd-June 6th-in
186 Germany, June 14th-July 8th in Belgium and July 10th-August 9th in Sweden), from 9 a.m. to 6 p.m. on sunny
187 days with low wind, and above 15°C. Flower visitation data were gathered along three parallel linear transects
188 (80m long and 3m wide) over 45 min (15 min per transect). The list of censused plants is shown in Appendix
189 S2 (Supporting Information) and the number of plants and pollinators censused in each grassland are given in
190 Table 1. We recorded the identity and number of insect contacts to flowers, considering only those (i.e. potential
191 pollination events) when an insect clearly touched the flower reproductive organs. Insects were either identified
192 in the field or collected (in Germany and Sweden) or photographed (in Belgium) for subsequent identification
193 by expert taxonomists. Licenses were not needed for fieldwork, and ethical approval was not required for the
194 research. Sampling completeness, estimated through the Chao2 index, was rather acceptable, being 68.9% and
195 48.87% for pollinator richness and plant-pollinator interactions, respectively.

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

202 **2.3 Plant reproductive performance**

203 We evaluated plant reproductive success by quantifying fruit set and viable seed set of two grassland
204 plant species that occur in all three regions: *Lotus corniculatus*, a common grassland generalist present in a
205 variety of habitats (van Treuren et al., 1993, Grant 1996), and a more habitat specialist *Salvia pratensis*
206 (Moughan et al., 2021). Both are referred hereafter as *Lotus* and *Salvia*. *Lotus* is self-incompatible, fully
207 dependent on insect pollination to produce viable seeds (Stephenson, 1984) and pollinated by different
208 pollinator functional groups whereas *Salvia* is self-compatible but needs pollinators to move pollen from the
209 anther to the ovary, being mainly pollinated by bees (van Treuren et al., 1993). At each grassland, we marked

210 up to 10 plant individuals, if available, per species, marking all flower buds of one of the inflorescences in
211 each individual. Before fruit dehiscence, we collected and counted the number of fruits and seeds in each.
212 Later in the laboratory, we used an X-ray test (Bruggink 2017) to assess seed viability, *i.e.*, whether seeds
213 contained a fully developed embryo and endosperm. The final evaluated variables were fruit set and viable
214 seed set.

215 **2.4 Estimation of network metrics**

216 We constructed quantitative bipartite networks using full-season data for each focal grassland, aiming
217 to provide a comprehensive and seasonal perspective on interactions, moving beyond daily analyses. While
218 this approach introduces the potential for 'forbidden links' due to varying flowering times, our analysis revealed
219 no significant difference in flowering turnover between ancient and restored grasslands (ANOVA: $F_{1,18} = 0.027$,
220 $P = 0.87$) or among regions (ANOVA: $F_{2,18} = 2.215$, $P = 0.14$). Therefore, the uniformity in flowering turnover
221 across grassland types and regions confirms the robustness of our results. Consequently, the overall outcomes
222 of our study are unlikely to be the result of a different probability of links between partners due to temporal
223 mismatches.

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

- 229 (i) *total number of different plant-pollinator interactions* (I);
- 230 (ii) *total number of visits* (V);
- 231 (iii) *mean number of links/species*;
- 232 (iv) *connectance* ($C = I/AP$), *i.e.*, the fraction of realized interactions in the network;
- 233 (v) *interaction evenness* (IE), which ranges from 0 to 1 with low values implying strong dominance
234 in the distribution of interactions such that some links are very strong (*i.e.* high interaction
235 frequencies) and many others weak;

236 (vi) *network specialization* (H'_2), which quantifies the degree of niche divergence of elements
237 within an entire bipartite network (Blüthgen, Menzel & Blüthgen, 2007) ranging from 0 (low
238 specialization, high niche overlap, high functional redundancy) to 1 (high specialization, low
239 niche overlap, low functional redundancy); and

240 (vii) *network modularity* (Q), which measures the extent to which species interactions are organized
241 into modules. Q values were estimated applying Newman's modularity adapted for quantitative
242 bipartite networks by Beckett (2016) and were corrected by comparing them to a reference
243 distribution derived from 100 random networks constructed with the *r2dtable* algorithm
244 (Patefield, 1981). The Q values in the randomizations were used to determine the z-score (Q_z).
245 This standardization allowed us to compare the different grasslands, because Q is sensitive to
246 network size and sampling intensity (Dormann & Strauss, 2014).

247 **2.5 Data analysis**

248 **2.5.1 Pollinator species assemblages**

249 By means of a linear model, we tested whether the type of grassland and amount of GI modified the
250 total number of pollinator species by using rarefaction curves. Rarefied species richness for each grassland
251 was estimated using the function “rarefy” implemented in the R package “vegan” (Oksanen et al., 2020, which
252 is based on Hurlbert's (1971) formulation. Curves were rescaled by the number of observations (i.e., number
253 of visits) to allow for species richness comparison. All models included grassland type and region as fixed
254 factors and amount of GI as a continuous predictor variable.

255 Multiple-site- β -diversity measures based on Bray-Curtis dissimilarity index were used to quantify
256 variation in pollinator species composition between grasslands. We employed the “*betapart*” R package
257 (Baselga et al., 2022) to compute three multiple-site beta diversity indices accounting for the: (i) balanced
258 variation ($\beta_{BC,BAL}$, individuals of some species in one grassland are replaced by the same number of individuals
259 of different species in another grassland) and (ii) abundance gradient components of dissimilarity ($\beta_{BC,GRA}$,
260 whereby some individuals are lost from one grassland to the other, (iii) and the sum of both values (β_{BC} , total
261 abundance-based dissimilarity). We then tested whether β_{BC} was related to type of grassland, GI amount, and

262 region using a Permutational Multivariate Analysis of Variance (PERMANOVA) on the Bray–Curtis
263 dissimilarity matrix. The analysis was implemented in the function “*adonis 2*” in R package “vegan” (Oksanen
264 et al., 2020) using 999 permutations. To assess whether differences in β -diversity were due to changes in the
265 main type of pollinator, we repeated the analyses but estimated multiple-site- β -diversity independently for
266 each pollinator functional group.

267 **2.5.2 Network topology**

268 Linear models were used to assess the effect of grassland type, amount of GI, and region on the different
269 network level metrics. Grassland type and region were included as fixed factors, and amount of GI and network
270 size (known to affect several network metrics; Blüthgen et al., 2008; Dormann & Strauss, 2014) as continuous
271 predictor variables. Given that the mean number of links per species correlated positively with network
272 connectance (C) and number of different interactions (I) ($r > 0.5$, $P < 0.001$), we used only the former as the
273 dependent variable. The remaining selected metrics at network level (i.e. H'_2 , IE and Q) were not significantly
274 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
275 measure of the total ‘volume’ of the pollination function. In this model, we included the variable “Habitat
276 Preference” and its interaction with type of grassland and GI. Habitat preference classified the visits according
277 to whether they were recorded on specialist grassland plant species or on generalist ones; a generalist was
278 considered a species found in different habitats whilst a specialist in only one habitat (Kimberley et al., 2021).
279 We used an identity link function with a normal distribution of residuals in all fitted linear models. Number of
280 visits, H'_2 , IE and Q_Z were ln-transformed to reach normality and homoscedasticity.

281 Model residuals were checked visually for normality and homogeneity of variance using diagnostic
282 plots (Zuur et al., 2009). The goodness-of-fit of the linear models was determined by means of the R-squared.
283 Linear models were fitted with the R packages “stats” (R Core Team, 2015) and “lme4” (Bates et al., 2015),
284 respectively. In the case of fitted models for network metrics, where we had a sample size of 24, a model
285 selection approach based on Akaike information criterion (AIC) was chosen. This approach is useful in the
286 case of low statistical power, as it manages a trade-off between model fit and model complexity (Burnham &
287 Anderson, 2002). AIC was used to evaluate full models and reduced models fitted for all variable
288 combinations. This approach selects the “best” model (i.e. that with the smallest AICc) and ranks the remaining

289 models based on their AICc value. Models with AICc > 4 relative to the best model were discarded, as they
290 have less statistical support (Burnham and Anderson, 2002). We also calculated the Akaike weight (w_i) of each
291 model as a proxy of model quality of adjustment (Burnham & Anderson, 2002). To quantify the relative
292 importance of the different predictors (w_+) on the network metrics, we summed w_i for each predictor across all
293 the models in which it occurred; the larger this sum, the more important a given variable is relative to the other
294 variables used in the same models (Burnham and Anderson, 2002). As there was some overlap in the circular
295 landscapes used as replicates (as indicated in the sampling design above), Moran's tests were conducted on
296 model residuals to assess spatial autocorrelation in the complete model. The results demonstrated no
297 statistically significant autocorrelation (all $P > 0.19$).

298 **2.5.3 Plant reproductive success**

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

304 **3. RESULTS**

305 **3.1 Composition of pollinator species assemblages**

306 We recorded a total of 7,105 pollinator visits across the three European regions (Appendix S3). Large
307 bees were the most active functional group (39.8 % of visits), followed by lepidopterans (21.6 %), coleopterans
308 (18.5 %), hoverflies (7.14 %), small bees (4.97 %), dipterans -excluding hoverflies- (4.85 %), wasps (1.69 %)
309 and ants (1.47 %). In contrast to the expected, no overall differences in pollination richness were detected
310 either between ancient and restored grasslands, and this was consistent across the three regions. Moreover, the
311 amount of GI was not found to significantly influence the number of pollinator species in each target grassland
312 (F -test: all $P > 0.05$, Table 1, Table S1 in Appendix S1).

313 Regarding β diversity, there was a wide variation in the composition of pollinator assemblages across
314 grasslands ($\beta_{BC}= 0.94$), and this dissimilarity was mainly driven by spatial replacement of species
315 ($\beta_{BC.BAL}=0.89$) rather than species loss from one grassland to another ($\beta_{BC.GRA}=0.05$). The PERMANOVA
316 analyses indicated that dissimilarity in species composition was partly due to the amount of GI, as grasslands
317 with similar GI values hosted similar pollinator assemblages (Table S2 in Appendix S1, PERMANOVA: $F_{1,19}$
318 $= 4.42$, $R^2= 0.12$, $P < 0.001$). The functional groups showing the greatest change in relation to a proportional
319 change of GI were small bees, lepidopterans, coleopterans, large bees, and dipterans (Figure 1, Table S2). In
320 contrast, GI did not affect the diversity of hoverflies, wasps and ants (Figure 1, Table S2: all $P > 0.05$).
321 Pollinator species composition also varied among the three regions (Table S2, PERMANOVA: $F_{1,19} = 6.93$,
322 $R^2= 0.36$, $P < 0.001$), which was mainly due to differences in species richness of coleopterans, large bees and
323 small bees between them (Figure 2A). The type of grassland did not influence pollinator assemblages (Table
324 S3 in Appendix S1, PERMANOVA: $F_{1,19} = 1.13$, $R^2= 0.03$, $P = 0.3$), as the proportion of each pollinator
325 functional group remained constant (Figure 2B).

326 **3.2 Changes in network topology**

327 Region and network size were included in most of the selected models (Table 2) and therefore had the
328 highest relative importance in explaining variation in network topology (Figure S2 in Appendix S1). GI and
329 grassland type were also key factors frequently integrated into these models (Table 2, Figure S2). The models
330 revealed that higher GI values decreased the total number of visits (Figure 3A), while restored grasslands
331 accumulated more visits than ancient ones (Figure 3B, Table S3). The impact of GI and grassland type on visit
332 numbers varied based on the habitat preferences of plant species (Figure 3B, Figure 3C, Table 2, Table S3).
333 Generalist plants received more visits in restored grasslands, with no significant differences for specialists
334 (Figure 3B). The negative effect of GI on visit numbers was more pronounced for specialists than for generalist
335 species (Table S3), and for restored than for ancient grasslands (Figure 3C, Table S3). Higher GI values led to
336 increased network specialisation (H'_2) while concurrently reducing the mean number of links per species and
337 network modularity (Q_2) (Figure 4A, Table 2, Table S3). Networks were more specialized and modular in
338 restored grasslands, while mean number of links per species also increased in restored pastures (Figures 3B,
339 Table 2, Table S3). Grassland type and GI were also chosen by the AIC criterion to account for variation in

340 interaction evenness, but neither of the models including GT or GI improved upon the intercept-only model
341 (Table 2). Furthermore, their explanatory power was low ($R^2 < 0.08$ in all models).

342 **3.3 Plant reproductive success**

343 Reproductive success was assessed for 159 *Lotus* and 42 *Salvia* individuals. *Salvia* produced more fruits
344 per flower (0.69 ± 0.05) than *Lotus* (0.36 ± 0.03) (Table 3: $F_{1,192} = 24.86$, $P < 0.001$), but grassland type did not
345 affect fruit set in either species (Table 3, $P > 0.005$). Fruit set increased with the number of pollinators visits
346 in *Salvia* but not in *Lotus* (Figure 4, Table 3: $F_{1,192} = 3.97$, $P < 0.05$). Seed viability was obtained from 123
347 individuals: 82 of *Lotus* and 41 of *Salvia*. Region and species were the only variables examined that had a
348 significant effect on seed viability (Table 3, Table S3). The significant species effect was because the mean
349 viable seed set was higher for *Lotus* than for *Salvia* (1.64 ± 0.41 vs 0.14 ± 0.2 , respectively) (Table 3: $F_{1,93} =$
350 5.76 , $P = 0.02$).

351 **DISCUSSION**

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

361 Here we show that this flexibility is dependent upon landscape connectivity and that such dependence
362 varies across pollinator functional groups. Specifically, our study provides evidence that the presence of GI
363 in the surrounding landscape is a key factor determining pollinator species composition, especially for small
364 and large bees, butterflies, beetles and dipterans. In contrast, GI was shown to be of minor relevance for
365 hoverflies, wasps and ants. Differences among pollinator functional groups in responses to landscape

366 connectivity were also documented by Öckinger et al. (2017) and by Rotchés-Ribalta et al. (2018). In
367 accordance with our results, the positive relationship between dissimilarity of GI and pollinator functional
368 groups was particularly notable for bees (Rotchés-Ribalta et al., 2018) and lepidopterans (Öckinger et al.,
369 2017), which can differ greatly in their effectiveness as pollinators (Ollerton, 2021).

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

375 Regarding the overall structure of the plant-pollinator networks, the total number of pollinator visits as
376 well as network specialization varied substantially between the two grassland types. It's worth noting that the
377 interaction between grassland type and GI was scarcely selected for nearly any model, indicating a limited
378 effect size, which implies that the effectiveness of restoration in terms of the pollination network structure was
379 not strongly influenced by the amount of GI. Restored grasslands received more pollinator visits than ancient
380 ones, which indicate that they are effective at attracting pollinators, but only to generalist plant species. This
381 led to more specialised networks, whereby pollinators tend to be more selective and do not use resources solely
382 on the basis of their abundance, resulting in a reduced niche overlap. This finding may imply that restored
383 grasslands are less functionally redundant (i.e., less resilient) than their ancient counterparts, and is consistent
384 with at least those of two previous studies who reported plant-pollinator interactions to be less robust on
385 restored than on ancient or reference sites (Forup et al., 2008; Williams, 2011). On the other hand, the amount
386 of GI was associated with networks exhibiting lower modularity. Specialization and modularity often exhibit
387 an inverse relationship as specialized pollinators tend to visit fewer plant species, leading to reduced interaction
388 diversity and complexity, reflected in a lower mean number of links per species. Additionally, higher values
389 of GI also correlated with a reduction in the total number of insect visits to flowers. These negative effects of
390 landscape connectivity were stronger for grassland-specialist than for grassland-generalist plants, which is
391 consistent with the effect of grassland type (restored vs ancient). Interestingly, the observed increase in fruit
392 set in the specialist *Salvia* with pollinator visits adds nuance to this narrative, hinting at potential pollination
393 limitations in specialist species within these grasslands. Thus, restored grasslands with low amounts of GI

394 were those promoting the highest number of insect visits to habitat-generalist plants, which might translate
395 into higher reproductive success of generalist plant species but not specialist ones. Such findings are consistent
396 with those of Kimberley et al. (2021) who reported that restored grasslands tend to have more generalist plant
397 species and a lower density of grassland specialists than ancient ones, leading to biotic homogenization.

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

416

417 **ACKNOWLEDGMENTS**

418 This research was funded through the 2015–2016 BiodivERsA COFUND call for research proposals, with the
419 national funders FORMAS (2016–01948), the Swedish Environmental Protection Agency (Naturvårdsverket),
420 the Belgian Science Policy Office (BelSPo, BELPSPO/BR/ 175/A1/FUNgreen), the Germany Federal
421 Ministry of Education and Research (Bundesministerium fuer Bildung und Forschung, FKZ: 01LC1619A) and

422 the Spanish Ministry of Science, Innovation and Universities (Ministerio de Ciencia, Innovación y
423 Universidades, PCIN- 2016-077). JMB was funded under UKCEH National Capability project 06895; DAPH
424 was contracted from Stockholm University as external scientist (contract reference 463). CLR was supported
425 by a Juan de la Cierva Formación postdoctoral fellowship (Ministerio de Economía, Industria y
426 Competitividad: FJCI-2015-24712). We are very grateful to all landowners that allowed us to work in their
427 fields. We thank Alberto García Calvente and Daniel Lenz for their field work in Belgium and Germany,
428 respectively; and Juan Carlos Alonso and Araceli Guillem for seed processing. We also acknowledge the
429 valuable work done by Óscar Luis Aguado, Santiago Bordera Sanjuán, Xavier Canyelles, Miguel Carles-Tolrá,
430 Carl-Cedric Coulianos, Leopoldo Castro, Xavier Espalader, Vicent Falcó, Miguel Ángel González Estévez,
431 Patrick Grootaert, Bert Gustafsson, Mattias Jentzsch, Emilia Narchuk, Nick Owens, Thomas Pape, Marc
432 Pollet, Adrian Pont, Carmen Rey del Castillo, Chris Saure, Axel Ssymank, Hanspeter Tschorsnig, Jeroen van
433 Steenis and Daniel Ventura who identified insects. Plant inventories in each of these countries were performed
434 by Maria Björk, Kasper van Acker, Robbe Cool and Lotje Vanhove, respectively. Maxi Bleicher and Irina
435 Weinberger (Ecology and Conservation Biology, Inst. of Plant Sciences, Univ. of Regensburg) did the seed
436 viability tests.

437 **CONFLICT OF INTEREST STAMENT**

438 The authors have no conflict of interest to declare.

439 **AUTHORS' CONTRIBUTIONS**

440 Anna Traveset, Silvia Santamaría, Carlos Lara-Romero and Gema Escribano Ávila conceived the ideas and
441 designed the methodology; Silvia Santamaría collected the plant-pollinator data at the three regions and
442 monitored fruiting in the field, while Patricia Krickl collected the seeds in Kallmünz, S.C in Sweden and O.H.
443 in Belgium Carlos Lara-Romero and Gema Escribano-Ávila analyzed the data; Sara Cousins, Peter Poschod,
444 and Olivier Honnay helped in the selection of study grasslands in Sweden, Germany and Belgium, respectively.
445 Adam Kimberley, James Bullock, Jan Plue and Danny Hooftman were heavily involved in project design both
446 in the acquisition phase and practically. Anna Traveset and Carlos Lara-Romero led the writing of the
447 manuscript with important contributions from Gema Escribano-Ávila and Silvia Santamaría. Statement on
448 inclusion: All authors contributed critically to the drafts and gave final approval for publication. Our study
449 brings together authors from several different countries, including scientists based in the country where the

450 study was carried out. All authors were engaged early on with the research and study design to ensure that the
451 diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature
452 published by scientists from the region was cited.

453 **DATA ACCESSIBILITY**

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

456 **REFERENCES**

457 Auffret, AG; Plue, J and Cousins, SAO. (2015) The spatial and temporal components of functional
458 connectivity in fragmented landscapes. *Ambio* 44 , S51-S59. [https://doi.org/10.1007/s13280-014-](https://doi.org/10.1007/s13280-014-0588-6)
459 [0588-6](https://doi.org/10.1007/s13280-014-0588-6)

460 Baselga, A. ; Gomez-Rodriguez, C.; Araujo, MB, [4] ; Castro-Insua, A. ; Arenas, M., Posada, D.; Vogler, AP.
461 (2022). Joint analysis of species and genetic variation to quantify the role of dispersal and
462 environmental constraints in community turnover. *Ecography* 5, e05808.
463 <https://doi.org/10.1111/ecog.05808>.

464 Bates D.; Mächler M.; Bolker B. & Walker S (2015). “Fitting Linear Mixed-Effects Models Using
465 lme4.” *Journal of Statistical Software*, 67, 1–48. <https://doi:10.18637/jss.v067.i01>.

466 Bengtsson, J. ; Bullock, JM.; Egoh, B.; Everson, C.; Everson, T; O'Connor, T. ; O'Farrell, PJ.; Smith,
467 HG. & Lindborg, R. (2019) Grasslands-more important for ecosystem services than you might think.
468 *Ecosphere*, 10: e02582. <https://doi.org/10.1002/ecs2.2582>

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

471 Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B., & Blüthgen, N. (2007). Specialization, Constraints, and
472 Conflicting Interests in Mutualistic Networks. *Current Biology*, 17, 341–346.
473 <https://doi.org/10.1016/j.cub.2006.12.039>

- 474 Blüthgen, N.; Frund, J.; Vazquez, DP. & Menzel, F. (2008) What do interaction network metrics tell us about
475 specialization and biological traits? *Ecology*, 89, 3387-3399. <https://doi.org/10.1890/07-2121.1>
- 476 Bruggink, H (2017) X-ray based seed analysis and sorting, Paper presented at ISTA conference.
- 477 Bullock, J.M., et al. (2011). Restoration of ecosystem services and biodiversity: conflicts and opportunities.
478 *Trends in Ecology & Evolution*, 26, 541–549. <https://doi.org/10.1016/j.tree.2011.06.011>
- 479 Burnham, K.P. & Anderson, D.R. (2002) Kullback-Leibler information as a basis for strong inference in
480 ecological studies. *Wildlife Research*, 28, 111-119. <https://doi.org/10.1071/WR99107>.
- 481
482 Clough, Y., ... Smith, H.G. (2014). Density of insect-pollinated grassland plants decreases with increasing
483 surrounding land-use intensity. *Ecology Letters*, 17, 1168–1177. <https://doi.org/10.1111/ele.12325>.
- 484 Cousins, S.A.O. (2006). Plant species richness in midfield islets and road verges—the effect of landscape
485 fragmentation. *Biological Conservation*, 127, 500–509. <https://doi.org/10.1016/j.biocon.2005.09.009>.
- 486 Cousins, S.A.O., et al. (2015). Regional-scale land-cover change during the 20th century and its
487 consequences for biodiversity. *Ambio* 44, 17–27. <https://doi.org/10.1007/s13280-014-0585-9>.
- 488 Cusser, S. & Goodell, K. (2013). Diversity and distribution of floral resources influence the restoration of
489 plant–pollinator networks on a reclaimed strip mine. *Restoration Ecology*, 21, 713–721.
490 <https://doi.org/10.1111/rec.12003>
- 491 Dániel-Ferreira, J., Fourcade, Y., Bommarco, R., Wissman, J., & Öckinger, E. (2023). Communities in
492 infrastructure habitats are species rich but only partly support species associated with semi-natural
493 grasslands. *Journal of Applied Ecology*, 00, 1– 12. <https://doi.org/10.1111/1365-2664.14378>
- 494 Devoto, M.; Bailey, S.; Craze, P. & Memmott, J. (2012). Understanding and planning ecological restoration
495 of plant–pollinator networks. *Ecology Letters*, 15, 319–328. [https://doi.org/10.1111/j.1461-
496 0248.2012.01740.x](https://doi.org/10.1111/j.1461-0248.2012.01740.x)

- 497 Dormann, C.F. & Strauss, R. (2014) A method for detecting modules in quantitative bipartite networks.
498 *Methods in Ecology & Evolution*, 5, 90-98. <https://doi.org/10.1111/2041-210X.12139>
- 499 Fenster C.B.; Armbruster, W.S.; Wilson, P.; Dudash, M.R.; Thomson, J.D. (2004) Pollination syndromes and
500 floral specialization. *Annual Review of Ecology, Evolution & Systematics*, 35, 375-403.
501 <https://doi.org/10.1146/annurev.ecolsys.34.011802.132347>
- 502 Forup, M.L.; Henson, K.S.E.; Craze, P.G.; Memmott, J. (2008). The restoration of ecological interactions:
503 plant-pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology*, 45, 742-
504 752. <https://doi.org/10.1111/j.1365-2664.2007.01390.x>
- 505 Garrido, P.; Marell, A. ; Ockinger, E.; Skarin, A.; Jansson, A.; Thulin, CG. (2019). Experimental rewilding
506 enhances grassland functional composition and pollinator habitat use. *Journal of Applied Ecology*, 56,
507 946–955. <https://doi.org/10.1111/1365-2664.13338>
- 508 Grant, W. F. (1996). Seed pod shattering in the genus *Lotus* (Fabaceae): a synthesis of diverse
509 evidence. *Canadian Journal of Plant Science*, 76(3), 447-456. <https://doi.org/10.4141/cjps96-079>
- 510 Habel, J.C., Habel, J.C.; Dengler, J.; Janisova, M.; Török, P.; Wellstein, C.; Wiezik, M. (2013). European
511 grassland ecosystems: threatened hotspots of biodiversity. *Biodiversity & Conservation*, 22, 2131–
512 2138. <https://doi.org/10.1007/s10531-013-0537-x>.
- 513 Holl, K. D., Luong, J. C., & Brancalion, P. H. (2022). Overcoming biotic homogenization in ecological
514 restoration. *Trends in Ecology & Evolution*, 37, 777-788. <https://doi.org/10.1016/j.tree.2022.05.002>
- 515 Hooftman, D.A.P. & Bullock, J.M. (2012). Mapping to inform conservation: A case study of changes in
516 semi-natural habitats and their connectivity over 70 years. *Biological Conservation*, 145, 30-38.
517 <https://doi.org/10.1016/j.biocon.2011.09.015>

518 Hooftman, D.A.P.; Bryan, E. & Bullock, J.M. (2016). Reductions in connectivity and habitat quality drive
519 local extinctions in a plant diversity hotspot. *Ecography*, 39, 583-592.
520 <https://doi.org/10.1111/ecog.01503>

521 Hooftman, D.A.P.; Kimberley, A.; Cousins, S.A.O.; Escibano-Avila, G.; Honnay, O.; Krickl, P.; Plue,
522 J.; Poschlod, P.; Traveset, A. & Bullock, J.M. (2021). Dispersal limitation, eutrophication and
523 propagule pressure constrain the conservation value of Grassland Green Infrastructure. *Biological*
524 *Conservation*, 258, 109152. <https://doi.org/10.1016/j.biocon.2021.109152>.

525 Hooftman, D.A.P.; Kimberley, A.; Cousins, S.A.O.; Santamaría, S.; Honnay, O. ; Krickl, P.; Plue,
526 J.; Poschlod, P.; Traveset, A. & Bullock, J.M. (2023) Could green infrastructure supplement
527 ecosystem service provision from semi-natural grasslands? *Journal of Environmental Management*,
528 328, 116952. <https://doi.org/10.1016/j.jenvman.2022.116952>

529 Hurlbert, S.H. (1971) Nonconcept of species diversity - critique and alternative parameters. *Ecology*, 52,
530 577- 586. <https://doi.org/10.2307/1934145>

531 Kaiser-Bunbury, C.; Mougil, J.; Whittington, A.E.; Valentin, T.; Gabriel, R.; Olesen, J.M.; Bluthgen, N.
532 (2017) Ecosystem restoration strengthens pollination network resilience and function. *Nature*, 542,
533 223-227. <https://doi.org/10.1038/nature21071>

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

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

- 542 Lehmail, T. A., Pagel, E., Poschlod, P., & Reisch, C. (2020). Surrounding landscape structures, rather than
543 habitat age, drive genetic variation of typical calcareous grassland plant species. *Landscape Ecology*,
544 35, 2881-2893.
- 545 Lindgren, J.; Lindborg, R. & Cousins, S.A.O.(2018). Local conditions in small habitats and surrounding
546 landscape are important for pollination services, biological pest control and seed predation.
547 *Agriculture, Ecosystems & Environment*, 251, 107–113. [https://doi.org/10.1016/j. agee.2017.09.025](https://doi.org/10.1016/j.agee.2017.09.025)
- 548 Moughan, J., McGinn, K. J., Jones, L., Rich, T. C., Waters, E., & de Vere, N. (2021). Biological Flora of the
549 British Isles: *Salvia pratensis*. *Journal of Ecology*, 109(12), 4171-4190.
550 <https://doi.org/10.1111/1365-2745.13805>
- 551 Noreika, N.; Bartomeus, I.; Winsa, M.; Bommarco, R. & Ockinger, E. (2019). Pollinator foraging flexibility
552 mediates rapid plant-pollinator network restoration in semi-natural grasslands. *Scientific Reports*, 9,
553 15473. <https://doi.org/10.1038/s41598-019-51912-4>
- 554 Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in
555 agricultural landscapes. *Journal of Applied Ecology*, 44, 50-59. [https://doi.org/10.1111/j.1365-
556 2664.2006.01250.x](https://doi.org/10.1111/j.1365-2664.2006.01250.x)
- 557 Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlenn, D.; Minchin, P.R.; O'Hara,
558 R.B.; Simpson, G.L.; Solymos, P.; Stevens, M.H.H.; Szoecs, E.; and Wagner, H. (2020). vegan:
559 Community Ecology Package. R package version 2.5-7. <https://cran.r-project.org/package=vegan>
- 560 Ollerton, J. 2021. *Pollinators & Pollination. Nature and Society*. Pelagic Publishing. Wales, UK.
- 561 Orford, K.A., et al. 2016. Modest enhancements to conventional grassland diversity improve the provision
562 of pollination services. *Journal of Applied Ecology*, 53, 906-915. [https://doi.org/10.1111/1365-
563 2664.12608](https://doi.org/10.1111/1365-2664.12608)
- 564 Patefield, W.M. (1981) Multivariate Linear Relationships - Maximum-Likelihood Estimation And
565 Regression Bounds. *Journal of the Royal Statistical Society Series B-Methodological*, 43, 342-352.

566
567 Plue, J.; Kimberley, A.; Bullock, J.M.; Hellemans, B.; Hooftman, D.A.P.; Krickl, P.; Leus, L.; Peeters,
568 G.; Poschlod, P.; Traveset, A.; Volckaert, F.; Cousins, S.A.O. & Honnay, O. (2022). Green
569 infrastructure can promote plant functional connectivity in a grassland species around fragmented
570 semi-natural grasslands in NW-Europe. *Ecography*, 2022, e06290.
571 <https://doi.org/10.1111/ecog.06290>

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

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

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

581 Rotchés-Ribalta et al. (2018). Associations between plant and pollinator communities under grassland
582 restoration respond mainly to landscape connectivity. *Journal of Applied Ecology*, 55, 2822–2833.
583 <https://doi.org/10.1111/1365-2664.13232>

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

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

588 Tarrant, S.; Ollerton, J.; Rahman, M.L.; Tarrant, J.; McCollin, D. (2013). Grassland Restoration on Landfill
589 Sites in the East Midlands, United Kingdom: An Evaluation of Floral Resources and Pollinating
590 Insects. *Restoration Ecology*, 21, 560–568. doi: <https://doi.org/10.1111/j.1526-100X.2012.00942.x>

- 591 Van Treuren, R., Bijlsma, R.; Ouborg, N.J. & Vandelden, W. (1993). The effects of population size and plant
592 density on outcrossing rates in locally endangered *Salvia pratensis*. *Evolution*, 47, 1094-1104.
593 <https://doi.org/10.1111/j.1558-5646.1993.tb02138.x>
- 594 Vázquez, D.P.; Poulin, R.; Krasnov, B.R. & Shenbrot, G.I. (2005). Species abundance and the distribution of
595 specialization in host–parasite interaction networks. *Journal of Animal Ecology*, 74, 946–955.
596 <https://doi.org/10.1111/j.1365-2656.2005.00992.x>
- 597 Williams, N.M. (2011) Restoration of Nontarget Species: Bee Communities and Pollination Function in
598 Riparian Forest. *Restoration Ecology*, 19, 450–459. [https://doi.org/10.1111/j.1526-
599 \[100X.2010.00707.x\]\(https://doi.org/10.1111/j.1526-100X.2010.00707.x\)](https://doi.org/10.1111/j.1526-100X.2010.00707.x)
- 600 Wilson, J.B.; Peet, R.K.; Dengler, J. & Partel, M. (2012) Plant species richness: the world records. *Journal*
601 *of Vegetation Science* 23, 796-802. <https://doi.org/10.1111/j.1654-1103.2012.01400.x>
- 602 Zuur, A.F.; Ieno, E.N. & Elphick C.S. (2009). A protocol for data exploration to avoid common statistical
603 problems. *Methods in Ecology & Evolution* 1, 3-14. [https://doi.org/10.1111/j.2041-
604 \[210X.2009.00001.x\]\(https://doi.org/10.1111/j.2041-210X.2009.00001.x\)](https://doi.org/10.1111/j.2041-210X.2009.00001.x)

Table 1. Network metrics and landscape information for the 24 focal semi-natural grasslands chosen to carry out the plant-pollinator interactions. GI is the total amount of hectares of grassland habitat within each target grassland. I: total number of different plant-pollinator interactions; V: total number of insect visits to flowers; C: network connectance; IE: interaction evenness; H'_2 : network specialization; I_{wp} : weighted linkage for plants; I_{wa} : weighted linkage for pollinators; Q: network modularity; Q_z : standardized network modularity

Grassland code	Grassland type	Region	GI	Plants	Pollinators	Rarefied pollinator species richness	I	V	C	Mean # Links per species	IE	H'_2	I_{wp}	I_{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

Table 2. Best-fitting regression models for explaining network level metrics. 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 (AICc). AICc measures the relative goodness of fit of a given model; the lower its value, the more likely this model is correct GT: grassland type, GI: green infrastructure, HP: habitat preference, NS: network size, RE: region.

	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 specialization (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

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*. Significant effects ($p < 0.05$) are indicated in bold. Parameter estimates fitted for fixed effects are provided as Supporting information (Table S4 in Appendix S1).

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		

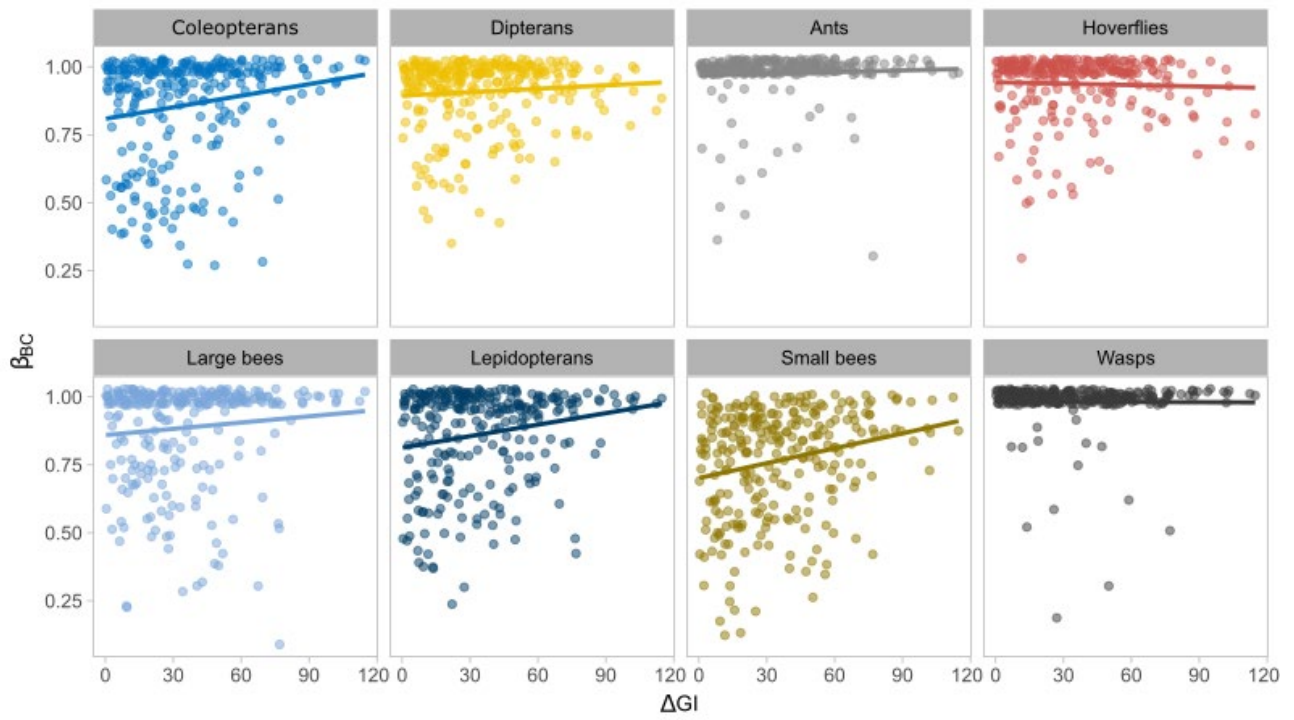


Figure 1. Effect of differences in the amount of green infrastructure (GI) between pairs of grasslands (Δ_{GI}) on multiple site β -diversity (β_{BC}) for each pollinator functional group: coleopterans, Dipterans, ants, hoverflies, large bees, lepidopterans, small bees and wasps.

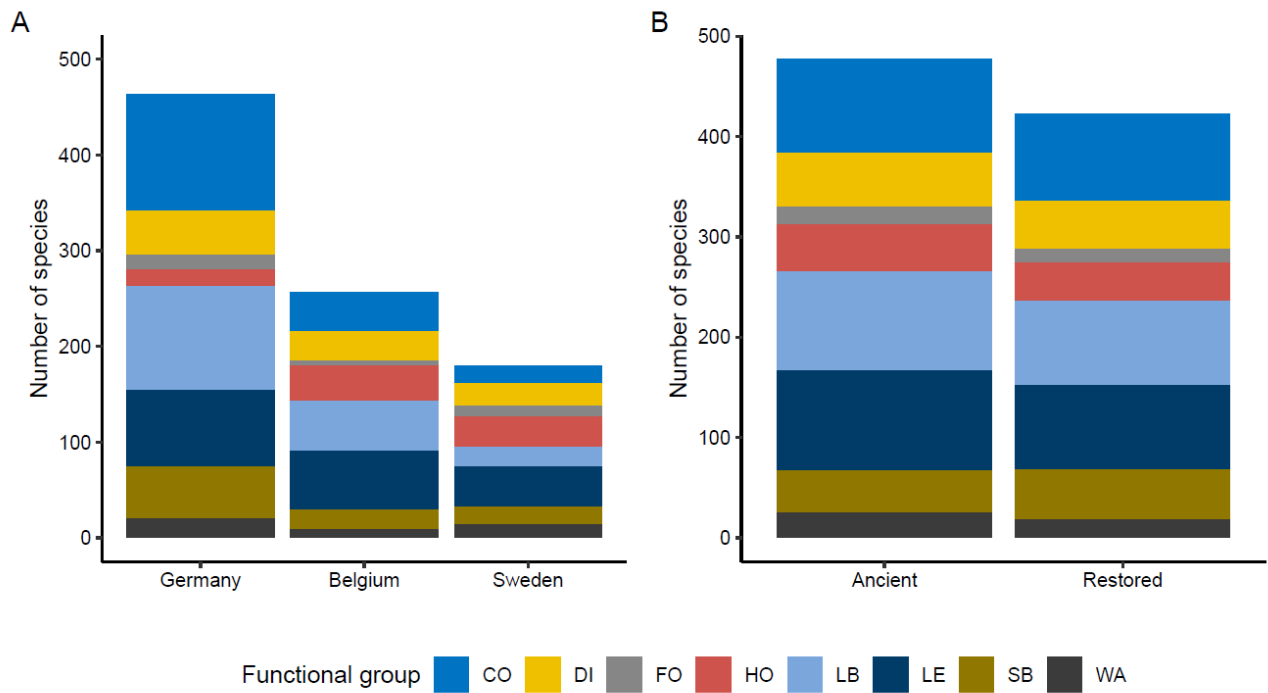


Figure 2. Species richness by pollinator functional group as a function of grassland type and region. Each colour represents a pollinator functional group: Coleopterans (CO), Dipterans (DI), ants (FO), hoverflies (HO), large bees (LB), lepidopterans (LE), small bees (SB) and wasps (WA). A) Distribution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

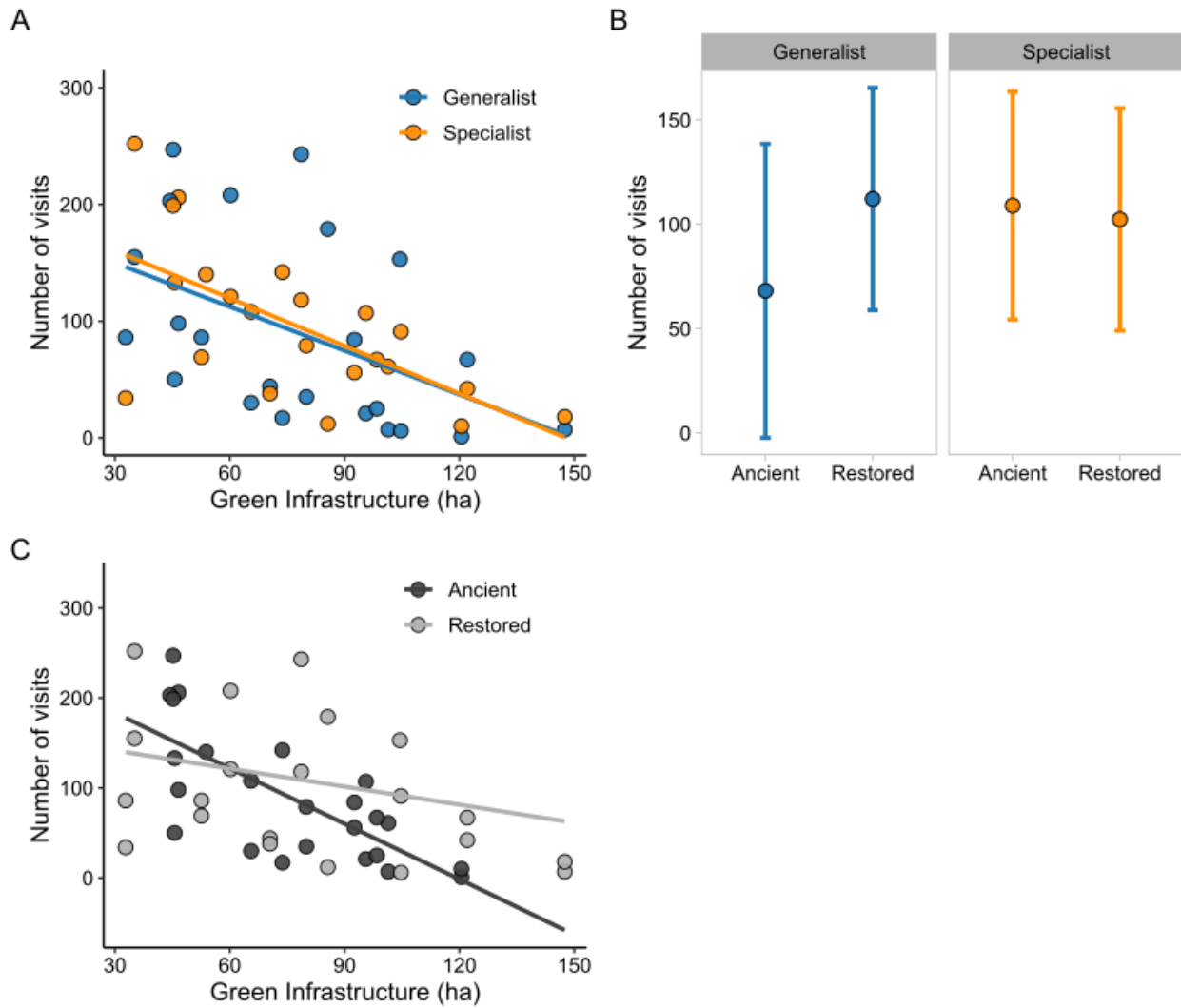


Figure 3. Impact of grassland type and green infrastructure on pollinator visits to specialist and generalist grassland plants. (A) Relationship between green infrastructure (GI) and the number of pollinator visits to specialist (blue dots) and generalist (orange dots) plants in the studied grasslands. 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 gray) and restored (light gray) grasslands. The trendline depicts a linear regression for each plant group.

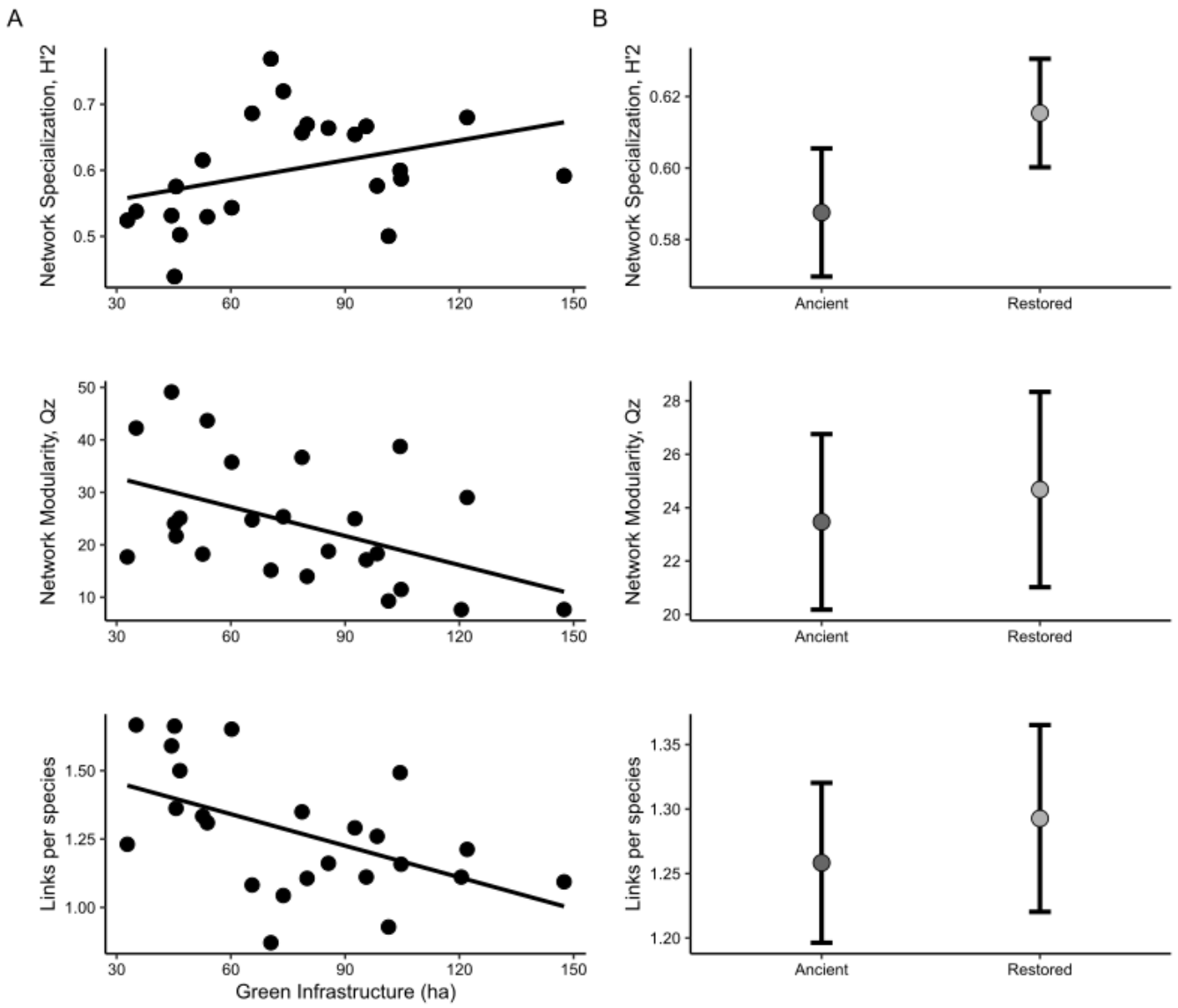


Figure 4. Influence of green GI and grassland type on network metrics. (A) The impact of GI on the network-level metrics in each grassland. The trendline illustrates the fitted linear regression. (B) A comparison of network-level metrics between ancient (dark gray) and restored (light gray) grasslands.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

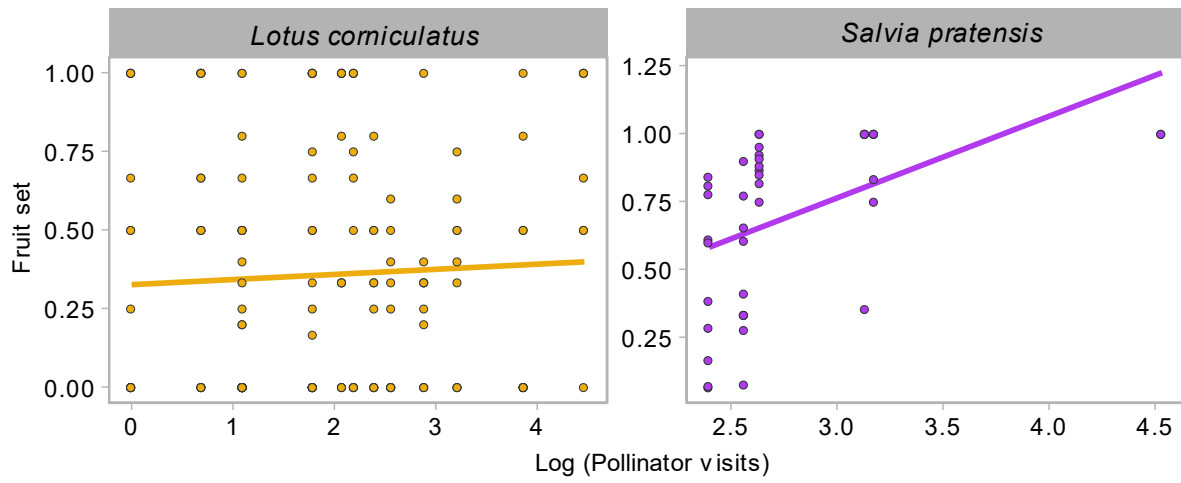


Figure 5. Association between number of pollinators visits and fruit set for the two model species: *Lotus corniculatus* (left) and *Salvia pratensis* (right).