SAFEGUARD

Report on the effectiveness of intervention strategies targeting complementary habitats needed by pollinators to complete their lifecycle

Deliverable D4.6

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Safeguard
Safeguarding European wild pollinators

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Summary

Safeguarding wild pollinators is crucial for maintaining biodiversity and ecosystem functioning in agricultural landscapes. Effective management practices include preserving diverse habitat types, particularly semi-natural ones, which provide complementary resources throughout the season, and implementing pollinator-friendly interventions such as flower strips and hedgerows. In this deliverable, we evaluated the effectiveness of different habitat types and pollinator-friendly interventions in supporting wild pollinator communities, also considering landscape composition and configuration, and temporal variability. By combining traditional diversity analysis with species-habitat network analysis, we aimed to understand how wild pollinators utilize resources across heterogeneous agricultural landscapes.

We conducted two case studies, one in Italy and one in Hungary. In Italy, we focused on permanent interventions, *i.e.*, hedgerows, in 14 agricultural landscapes. We sampled wild pollinators using pan traps placed across different habitat types (crop field margins, fallows, hedgerows, and road verges) during three sampling periods from May to July 2020. In Hungary, we established flower fields and strips in 24 landscapes with contrasting landscape compositions. We sampled wild pollinators using pan traps yearly, from 2020 to 2023. In both case studies, we focused on wild bees, which emerged as the most abundant pollinator group collected.

We found that the contribution of different habitat types to wild bee abundance and richness was variable, with semi-natural habitats and specific agricultural habitats showing higher potential for bee conservation. However, species composition was similar across different habitats, suggesting that agricultural landscapes act as a filter, favouring generalist bee species. As a result, species-habitat networks were generally robust to potential habitat loss, despite this resilience was partly affected by complex interaction with temporal variability and landscape composition and configuration. Seasonal and inter-annual variations significantly affected pollinator abundance and richness, as well as network characteristics, highlighting the dynamic nature of pollinator communities and foraging behaviour across landscapes. Single pollinator-friendly interventions had limited direct impact on wild bees at the landscape scale, potentially due to their floral composition and placement within landscapes.

Understanding these dynamics is essential for developing effective conservation strategies to sustain pollinators within agricultural ecosystems. Based on our findings, we recommend management practices to support pollinator communities and enhance ecosystem resilience within agricultural landscapes, including: enhancing landscape heterogeneity, as specific habitats supported higher abundance and richness of wild pollinators; exploring the role of overlooked habitats in pollinator conservation, such as reed beds and wetland habitats, which emerged as promising habitats for wild bee conservation; improving the management of road verges, the least beneficial habitat for wild bees in both studies, given their extensive coverage across landscapes; ensuring optimal design and positioning of pollinator-friendly interventions to maximize their effectiveness; considering multiple pollinator guilds, as different pollinator groups may respond differently to environmental factors; implementing network analysis in conservation planning, for example to explore robustness of communities to habitat loss and the importance of specific patches; and incorporating seasonal and inter-annual changes in conservation strategies and emphasizing long-term monitoring.

List of abbreviations

EU	**European Union**
MFC	**Mass-flowering crop**

1. Introduction

The conservation of wild pollinator insects is crucial for maintaining biodiversity and ecosystem functioning. A fundamental approach to safeguarding wild pollinator communities is to preserve different habitat types in landscapes, which could provide complementary floral and nesting resources essential for the survival and well-being of multiple wild pollinator guilds. In particular, semi-natural habitats such as forests and grasslands, characterized by a high cover and diversity of floral resources, are known to sustain greater pollinator abundance and richness compared to agricultural habitats (Eeraerts et al. 2021; Vujanović et al. 2023; Ammann et al. 2024). A mosaic of semi-natural habitats in landscapes, including meadows, flower strips, and hedgerows, fosters diverse bee communities by hosting unique plant communities that cater to unique sets of pollinator species (Maurer et al. 2022). By providing access to a spatially and temporally heterogeneous supply of floral resources, which can complement those offered by crops, these habitats not only enhance pollinator reproduction and developmental success (Filipiak 2019; Klaus et al. 2021a) but could also mitigate the impact of additional environmental stressors (Vanderplanck et al. 2019, Bihaly et al. 2024). However, the ongoing intensification of agricultural landscapes results in the loss of these central habitats, threatening pollinators by reducing essential floral and nesting resources.

To counteract these negative effects, pollinator-friendly interventions have been widely implemented in agricultural landscapes. Among these, sown flower strips and permanent hedgerows are particularly effective in increasing both pollinator abundance and richness (Morandin and Kremen 2013; Tschumi et al. 2016; von Königslöw et al. 2022; Donkersley et al. 2023). Flower strips typically consist of a mix of annual and perennial herbaceous plants (Jachowicz and Sigsgaard 2025), while hedgerows are more structurally complex, with herbs and shrubs often interspersed with trees, allowing insects to access diversified floral resources throughout the year. Flower strips have been shown to also enhance the reproductive success of bees and decrease the parasitism rate (Ganser et al. 2021), and in some contexts, they could be more beneficial for pollinators than hedgerows (von Königslöw et al. 2022). However, hedgerows play a crucial role in providing nesting and overwintering sites (M’Gonigle et al. 2015), especially for specific pollinator guilds, such as hoverflies (Alison et al. 2022). Therefore, both flower strips and hedgerows could be suitable and complementary conservation measures to support pollinators in agricultural landscapes.

Beyond local conservation measures, the composition and spatial configuration of the surrounding landscape significantly influence pollinator communities. Landscapes with a high proportion of semi-natural habitats and high edge density generally support higher wild bee abundance and richness (Eeraerts et al. 2019; Proesmans et al. 2019a; Martin et al. 2019; Pardo and Borges 2020; Klaus et al. 2021b). However, the effects of landscape characteristics on pollinators are often complex and might also impact the effectiveness of pollinator-friendly interventions. For example, the positive effects of flower strips are generally more pronounced in landscapes with low habitat quality (Pérez-Sánchez et al. 2023), and wild bee reproduction increases in landscapes with flower strips only when characterized by small fields with long field borders (Geppert et al. 2020). Additionally, the placement of semi-natural habitats and pollinator-friendly interventions in landscapes is critical, as pollinator richness and visitation rates strongly decline with increasing distance from these areas (Ricketts et al. 2008; Albrecht et al. 2020). Given these intricate landscape-level effects, integrating landscape composition and configuration into sustainable land management strategies is essential for maintaining healthy pollinator communities.

The exploitation of habitats in landscapes by pollinators is dynamic, responding to intra-annual (seasonal) and inter-annual variations in floral resource availability. The relative importance of habitats in landscapes fluctuates throughout the season, as pollinators shift from woody resources to herbaceous plants across the season (Ammann et al. 2024), with significant differences among pollinator guilds (Cole et al. 2017). Extensively managed meadows provide continuous resources for wild pollinators, while the importance of flower strips increases as the season progresses (Maurer et al. 2022). Seasonal variation can also interact with landscape composition, *e.g.*, landscapes with a high proportion of crops, usually inhospitable for pollinators, may support pollinators early in the season, when mass-flowering crops are blooming (Galpern et al. 2021). For inter-annual variation, the effectiveness of pollinator-friendly interventions may depend on the time since their establishment, with young flower strips typically being especially attractive for pollinators (Krimmer et al. 2019; Albrecht et al. 2021). In addition, environmental factors such as temperature, humidity and extreme events can influence pollinator survival, emergence and activity. Pollinator emergence is positively correlated with humidity levels (Rohde and Pilliod 2021), while extreme events such as heat waves and droughts can alter pollinator abundance and composition compared to normal years (Zoller et al. 2020), also because of reduced nectar and pollen availability (Jaworski et al. 2022).

Considering all these factors and how they interact with each other, it is clear how managing multiple habitats for the conservation of multiple pollinator species and guilds can be challenging. Recently, ecological network analysis has been proposed as a tool to understand these intricate spatial interactions (Marini et al. 2019). Species-habitat networks and their associated metrics and indices can provide insights into how pollinators use resources at the landscape scale, informing conservation strategies (Saunders and Rader 2019; Cappellari and Marini 2021; Lami et al. 2021; Dong et al. 2025). Network-level metrics can reveal structural properties of the whole species-habitat networks, for example, network specialization can be useful for understanding pollinator selectivity for habitats, and network robustness can be used to assess the implications of habitat loss on pollinator communities (Marini et al. 2019; Palmeirim et al. 2022; Hao et al. 2024). Additionally, node-level indices, such as centrality and strength, can describe properties of single habitat patches within the network, highlighting the importance of specific habitats and patches in supporting pollinators across the whole landscape (Marini et al. 2019).

This deliverable aims to investigate the role of different habitat types and pollinator-friendly interventions in supporting wild pollinator communities in agricultural landscapes, and how landscape composition and configuration, as well as temporal variability, shape species-habitat networks, through two case studies. The first case study was conducted in north-eastern Italy and focused on permanent interventions, *i.e.*, hedgerows. We selected 14 landscapes and 8-16 sites per landscape belonging to four habitat types, *i.e.*, crop field margin, fallow, hedgerow, and road verge. We sampled pollinators using coloured pan traps activated for 48 hours, repeating samplings three times, from May to July 2020. The second case study was conducted in Hungary and focused on flower strips and flower fields (Báldi et al. 2022). We selected 24 landscapes characterized by different covers of semi-natural areas. Landscapes were organized in triplets, with each triplet having one control landscape, one landscape sown with a flower field, and one landscape sown with three flower strips. Within each landscape, we selected 24 sampling sites arranged in a grid belonging to four habitat types, *i.e.*, arable land, grassland, reed bed, and road verge. Similar to the previous case study, we sampled pollinators using pan traps activated for 48 hours. Samplings were conducted in July and repeated across four consecutive years, from 2020 to 2023. Our analysis focused on wild bees, which emerged as the most abundant pollinator group collected. We analysed how wild bee abundance and richness varied in the sampled habitat types, with a specific focus on pollinator-friendly interventions, and how these effects were mediated by temporal variability. Additionally, we built bipartite and unipartite species-habitat networks and focused on both network-level metrics (network specialization and robustness to patch removal) and node-level metrics (patch centrality and strength) to understand how the foraging behaviour of pollinators at the landscape scale was affected by landscape characteristics and local variables.

2. Materials and methods

2.1. Case study 1: Italy

2.1.1. Study area

The study was conducted in the Veneto region (north-eastern Italy) (Figure 1a). Climate in the study area is continental, with a mean annual temperature of about 14 °C. Mean minimum temperatures range between 0 °C in January and 18 °C in July, while mean maximum temperatures range between 8 °C in January and 30 °C in July. Total precipitation is about 900 mm per year, with two peaks, one in spring and one in autumn. The landscape is intensively managed and dominated by crops (85%), mostly soy, wheat, maize, and mass-flowering crops such as sunflower.

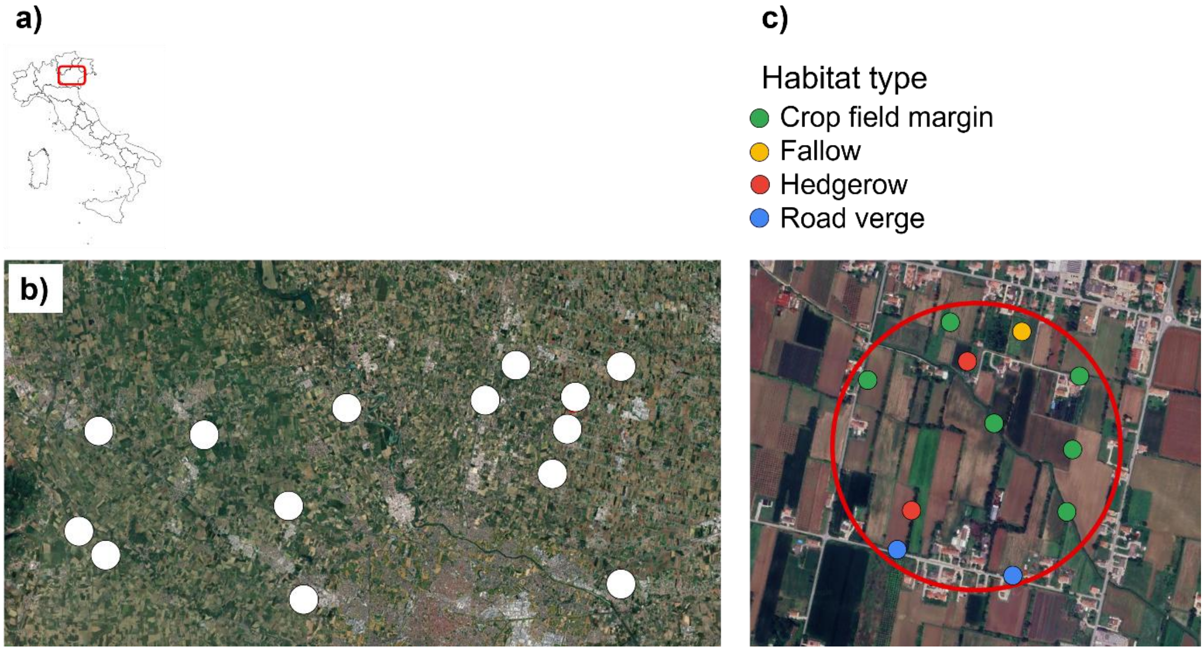

Figure 1: a) Sampling region in Italy. b) Map showing the 14 sampled landscapes. c) Example of one sampled landscape, with sites coloured based on the habitat type. Background images from Google Earth (2024).

2.1.2. Sampling design

Field activities were carried out in 14 agricultural landscapes of 360-m radius (Figure 1b). Within each landscape, we selected 8-16 sampling sites (patches) belonging to four habitat types: crop field margins, fallows, hedgerows, and road verges (Figure 1c). The number of sampling sites for each habitat in each landscape reflected landscape composition.

2.1.3. Landscape composition and configuration

For each landscape, we calculated the cover of the main habitat types within 360-m radius buffers. Polygons of urban areas, agricultural land, mass-flowering crops (MFCs; *i.e.*, sunflower, soy, oilseed rape, and alfalfa), and semi-natural habitats were manually digitized in Google Earth Pro (Google Earth 7.3.6.10201). We then focused on both landscape composition, calculating the cover of the main habitat types in the landscape, and configuration, calculating the number of crop patches within each landscape.

2.1.4. Wild pollinator sampling

We sampled wild bees (Hymenoptera: Apoidea: Anthophila) and hoverflies (Diptera: Syrphidae) using pan traps. At each sampling site, we placed three coloured pan traps (yellow, blue, and white; 750 ml, Ø 12.5 cm, h 4.5 cm), 1 m apart from each other, filled with water and a drop of biodegradable dish soap with no fragrance. Pan traps were placed on the ground, in areas with short grass, so that they were visible to pollinators. Pan traps were exposed for 48 hours during sunny days, with low wind and temperatures > 20 °C. Collected insects were stored in vials filled with 70% ethanol and were morphologically identified to the species or morphospecies level by taxonomists. Wild pollinator samplings were repeated three times, once per month, between May and July 2020.

2.1.5. Species-habitat networks

Using the collected data, we built two types of networks for each landscape and sampling month to describe how wild bees use resources across landscapes: a) a bipartite species-habitat weighted network, with nodes represented by wild bee species and habitat patches, and links represented by visits of wild bees to habitat patches (Figure 2a); and b) a unipartite weighted network, with nodes represented by habitat patches and links represented by wild bee species shared among patches (Figure 2b). Since we collected very few hoverfly individuals (277 individuals in total, see General results), we opted to include only wild bees in the following analyses and models. We focused on both node-level indices and network-level metrics.

At the node level, we calculated patch centrality (starting from unipartite networks) and patch strength (starting from bipartite networks). For patch centrality, we calculated weighted degree centrality, an index which specifies the role played by each patch within the network, highlighting the focal ones. It is based on both the number of connections with other patches and the average weight of these connections, adjusted by an α parameter (Opsahl et al. 2010). We set the α parameter to 0.5, so patches with a higher number of connections have higher weighted degree centrality values (Rodríguez-Rodríguez et al. 2017). A high centrality value indicates a patch which hosts many generalist species, while a low centrality value indicates a patch which hosts specialist or few species. In addition, we calculated patch strength, defined as the sum of the dependences of the wild bee species visiting the patch (Bascompte et al. 2006). The dependence of a wild bee species is defined as the proportion of individuals of the species visiting the patch. Therefore, strength can be used to rank patches based on their importance within the network. To allow comparisons among patches, we normalized the strength value by dividing it by the number of species collected at each patch.

At the network level, we calculated network specialization (H2') and network robustness to patch removal. H2′, the standardized two-dimensional Shannon entropy, indicates how habitats are partitioned among pollinator species (Blüthgen et al. 2006), ranging from 0 (completely generalized network) to 1 (completely specialized network). Network robustness quantifies the stability of a network to patch removal, *i.e.*, whether a high number of pollinator species would be lost in case of habitat loss or not. Network robustness to patch removal was calculated using two approaches (Luza et al. 2024): a) by first removing the least-visited patches, and b) by removing patches in a specific order, based on the probability of habitat loss, *i.e.*, starting with semi-natural habitat patches followed by managed habitat patches (order: hedgerows, fallows, crop field margins, and road verges). Within each habitat type, sites were then randomly ordered and removed. The index ranges from 0 (highly unstable network) to 1 (highly stable network).

All metric calculations and statistical analysis were conducted in R (R Core Team 2019). Node- and network-level metrics were calculated using the *bipartite* (Dormann et al. 2017) and *tnet* packages (Opsahl 2015).

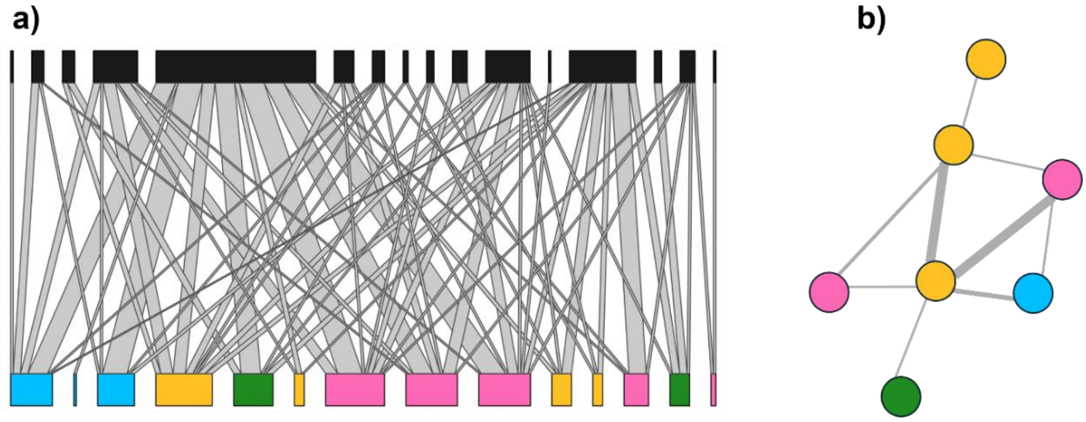

Figure 2: a) Example of a bipartite species-habitat weighted network, with top nodes representing species (wild bees), bottom nodes representing habitat patches, and links representing weighted interactions between pollinators and habitat patches (*i.e.*, number of pollinators of each species visiting each habitat patch). b) Example of a unipartite weighted network, with nodes representing habitat patches, and links representing pollinator species shared among patches. Colours of habitat patches represent different habitat types.

2.1.6. Statistical analysis

First, we assessed sampling completeness through species accumulation curves using the *accumcomp* function in the R package *BiodiversityR* (Kindt and Coe 2005).

Second, we visually analyzed species composition of wild bees across the four habitat types using nonmetric multidimensional scaling (NMDS, Bray-Curtis dissimilarity index), summing the species abundances across the three sampling months. NMDS analysis was performed using the function *metaMDS* in the R package *vegan* (Oksanen et al. 2019).

Third, we tested how abundance and richness of wild bees changed across the four sampled habitat types throughout the sampling season. We built two linear mixed-effect models including wild bee abundance (Model 1) and wild bee richness (Model 2) as response variables, and the interaction between habitat type (crop field margin, fallow, hedgerow, and road verge) and sampling month (May, June, and July) as explanatory variable. Both models also included the nested random effect of site within landscape. Wild bee abundance was logarithmically transformed to meet the assumption of normally distributed residuals. Models were built using the function *lme* in the R package *nlme* (Pinheiro et al. 2019). All figures were built using the R package *ggplot2* (Wickham 2016).

Fourth, we tested how patch-level indices changed in the four habitat types throughout the sampling season. We built two linear mixed-effect models including patch weighted degree centrality (Model 3) and patch normalized strength (Model 4) as response variables, and the interaction between habitat type (crop field margin, fallow, hedgerow, and road verge) and sampling month (May, June, and July) as explanatory variable. Both models also included the nested random effect of site within landscape. Patch normalized strength was logarithmically transformed to meet the assumption of normally distributed residuals.

Last, we tested how network metrics changed throughout the season and with landscape features. We built three linear mixed-effect models including network metrics as response variables, *i.e.*, network specialization H2' (Model 6), network robustness to patch removal calculated by first removing the least-visited patches (Model 7), and network robustness to patch removal calculated by removing patches in a specific order, based on the probability of habitat loss (Model 8). Explanatory variables were the interaction between the percentage of semi-natural areas in landscapes and the sampling month, between the percentage of MFCs in landscapes and the sampling month, and between the number of crop patches in landscapes and the sampling month. Models also included the nested random effect of site within landscape. For these models, we only included landscapes where at least 30 specimens were collected in total, and with at least five sites where a minimum of five pollinator specimens were collected.

For a summary of all models, see Table 1a.

Table 1: Summary of the linear mixed-effect model for a) case study 1 (Italy) and b) case study 2 (Hungary).

Model	Response variable	Explanatory variable(s)	Random effect
a) Case study 1: Italy			
Model 1	Wild bee abundance	Habitat type × Sampling month	Landscape / site
Model 2	Wild bee richness	Habitat type × Sampling month	Landscape / site
Model 3	Patch weighted degree centrality	Habitat type × Sampling month	Landscape / site
Model 4	Patch normalized strength	Habitat type × Sampling month	Landscape / site
Model 6	Network specialization	Semi-natural % × Sampling month + Mass-flowering crop % × Sampling month + Number of crop patches × Sampling month	Landscape / site
Model 7	Network robustness to patch removal (visits)	Semi-natural % × Sampling month + Mass-flowering crop % × Sampling month + Number of crop patches × Sampling month	Landscape / site
Model 8	Network robustness to patch removal (habitat)	Semi-natural % × Sampling month + Mass-flowering crop % × Sampling month + Number of crop patches × Sampling month	Landscape / site
b) Case study 2: Hungary			
Model 1	Wild bee abundance (log+1)	Habitat type × Year	Landscape / site
Model 2	Wild bee richness (log+10)	Habitat type × Year	Landscape / site
Model 3	Wild bee abundance (log+1)	Distance from intervention × Year	Landscape / site
Model 4	Wild bee richness (log+10)	Distance from intervention × Year	Landscape / site

Model 5	Patch weighted centrality	Habitat type × Year	Landscape / site
Model 6	Patch normalized strength (log)	Habitat type × Year	Landscape / site
Model 7	Patch weighted centrality	Distance from intervention × Year	Landscape / site
Model 8	Patch normalized strength (log)	Distance from intervention × Year	Landscape / site
Model 9	Network specialization	Intervention type × Year + Landscape type × Year + Intervention type × Year	Landscape / site
Model 10	Network robustness to patch removal (visits)	Intervention type × Year + Landscape type × Year + Intervention type × Year	Landscape / site
Model 11	Network robustness to patch removal (habitat)	Intervention type × Year + Landscape type × Year + Intervention type × Year	Landscape / site

2.2. Case study 2: Hungary

2.2.1. Sampling design

We selected 24 circular landscapes of 500-m radius within homogeneous (N=12, <10% of semi-natural habitats) or heterogeneous (N = 12, 40-60% of semi-natural habitats) landscapes in Central Hungary (Figure 3a). Within 16 landscapes, we sowed 0.5 ha with a wildflower seed mixture in February 2020. These sown parcels either consisted of a single large field (8 landscapes) or three smaller, spatially associated strips about 100-150 m apart (8 landscapes), yet of 0.5 ha in total area. Further 8 landscapes without flowering fields or strips served as control landscapes (Figure 3b). Within each landscape, we established 24 equally distributed sampling sites (patches) arranged in a grid (Figure 4a).

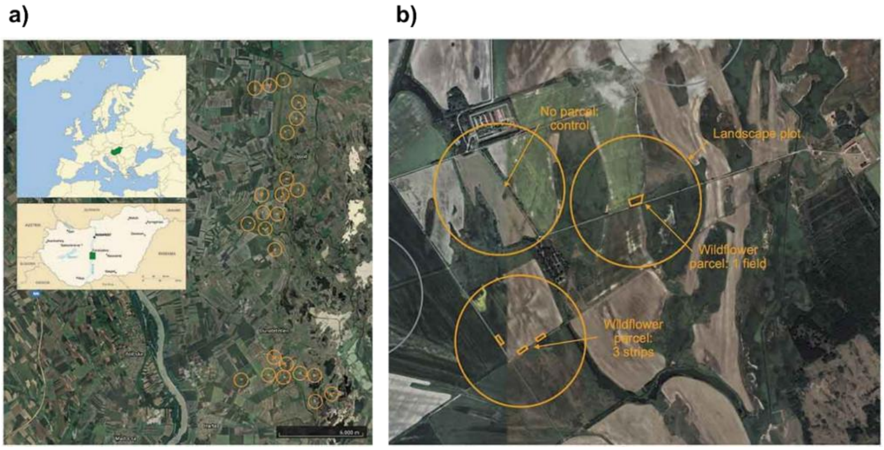

Figure 3: a) The study design consisted of 24 circular landscape plots in Central Hungary. b) Landscapes were grouped into trios with a sown wildflower field, a triplet of sown wildflower strips, and a control. Background images from Google Earth (2021).

2.2.2. Wild pollinator sampling

We sampled wild bees (Hymenoptera: Apoidea: Anthophila) using pan traps. At each site, a painted yellow plastic pan filled with water and a drop of detergent was mounted on top of a pole (Figure 4b). Pan traps were exposed for 48 hours during sunny days, with low wind and temperatures > 20 °C. Collected bees were stored in vials filled with 70% ethanol and were morphologically identified to the species or morphospecies level by taxonomists. Wild bee samplings were repeated for four consecutive years (2020-2023).

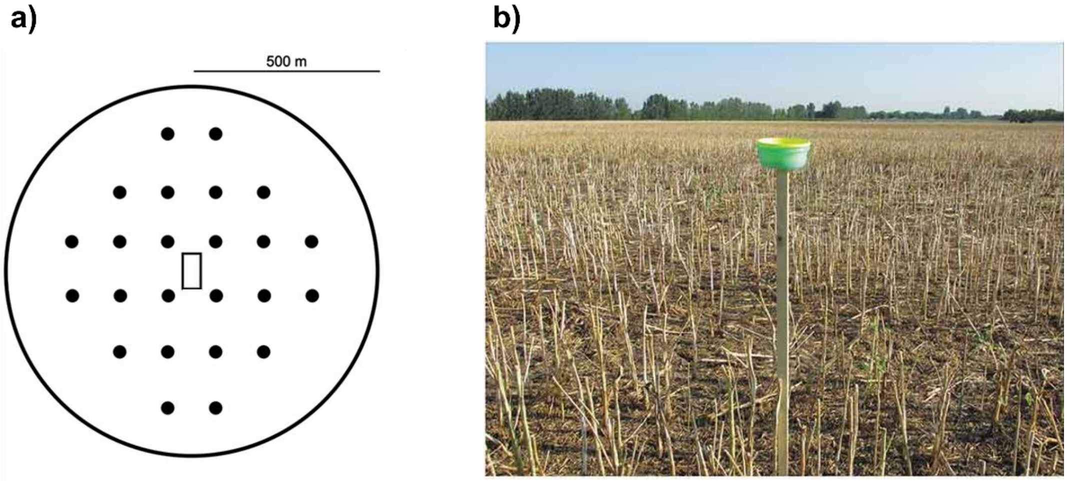

Figure 4: a) Schematic representation of a landscape plot with a wildflower parcel (rectangle), showing the distribution of pan traps (dots). b) Pan trap mounted on a pole in a harvested oilseed rape field (photographer: András Báldi).

2.2.3. Species-habitat networks

Similar to the previous case study, for each landscape and sampling year we built one bipartite species-habitat weighted network (with nodes represented by wild bee species and habitat patches, and links represented by visits of wild bees to habitat patches) and one unipartite weighted network (with nodes represented by habitat patches and links represented by wild bee species shared among patches). At the node-level, we calculated weighted degree centrality and normalized strength for each patch within each network. At the network-level, we calculated three metrics: a) network specialization (H2'), b) network robustness to patch removal calculated by first removing the least-visited patches, and c) network robustness to patch removal calculated by removing patches in a specific order, based on the probability of habitat loss, *i.e.*, starting with semi-natural habitat patches followed by managed habitat patches (order: grasslands, reed bed, road verges, and arable land).

2.2.4. Statistical analysis

First, we assessed sampling completeness through species accumulation curves using the *accumcomp* function in the R package *BiodiversityR* (Kindt and Coe 2005).

Second, we visually analyzed species composition of wild bees across the four habitat types using nonmetric multidimensional scaling (NMDS, Bray-Curtis index), summing the species abundances across the four sampling years. NMDS analysis was performed using the function *metaMDS* in the R package *vegan* (Oksanen et al. 2019).

Third, we tested how abundance and richness of wild bees changed in the four sampled habitat types across the four years. We built two linear mixed-effect models including wild bee abundance (Model 1) and wild bee richness (Model 2) as response variables, and the interaction between habitat type (arable land, grassland, reed bed, and road verge) and sampling year (2020, 2021, 2022, 2023) as explanatory variable. Both models also included the nested random effect of site within landscape. Wild bee abundance and richness were logarithmically transformed to meet the assumption of normally distributed residuals.

Fourth, we tested how abundance and richness of wild bees were affected by the distance from the pollinator-friendly interventions within landscapes. We built two linear mixed-effect models including wild bee abundance (Model 3) and wild bee richness (Model 4) as response variables, and the interaction between the distance from pollinator-friendly interventions (category: 1, 2, 3, 4) and the sampling year (2020, 2021, 2022, 2023) as explanatory variable. Both models also included the nested random effect of site within landscape. Wild bee abundance and richness were logarithmically transformed to meet the assumption of normally distributed residuals. For these models, only landscapes with pollinator-friendly interventions (N=16) were included.

Fifth, we repeated similar analysis for patch-level indices. We built two linear mixed-effect models including patch weighted degree centrality (Model 5) and patch normalized strength (Model 6) as response variables, and the interaction between habitat type (arable land, grassland, reed bed, and road verge) and sampling year (2020, 2021, 2022, 2023) as explanatory variable. In addition, we built two linear mixed-effect models including patch weighted degree centrality (Model 7) and patch normalized strength (Model 8) as response variables, and the interaction between the distance from pollinator-friendly interventions (category: 1, 2, 3, 4) and sampling year (2020, 2021, 2022, 2023) as explanatory variable. All four models also included the nested random effect of site within landscape. Patch normalized strength was logarithmically transformed to meet the assumption of normally distributed residuals. For models 7 and 8, only landscapes with pollinator-friendly interventions (N=16) were included.

Last, we tested how network metrics changed across the four sampling years based on landscape type and pollinator-friendly intervention type. We built four linear mixed-effect models including network metrics as response variables, *i.e.*, network specialization H2’ (Model 9), network robustness to patch removal calculated by first removing the least-visited patches (Model 10), and network robustness to patch removal calculated by removing patches in a specific order, based on the probability of habitat loss (Model 11). Explanatory variables were the interaction between landscape type (heterogeneous and homogeneous) and sampling year, between pollinator-friendly intervention type (control, flower field, flower strips) and sampling year, and between landscape type and pollinator-friendly intervention type. Models also included the nested random effect of site within landscape. For these models, we only included landscapes where at least 30 specimens were collected in total, and with at least five sites where a minimum of five pollinator specimens were collected.

For a summary of all models, see Table 1b.

3. Results

3.1. Case study 1: Italy

3.1.1. General results

In total, we collected 4,310 pollinators belonging to 108 species (Table 2). Most of these pollinators were wild bees, accounting for 4,033 individuals belonging to 78 species. The most abundant and common species belonged to the Halictidae family, *i.e.*, *Lasioglossum glabriusculum* (1,468 individuals collected in 305 sampling occasions, *i.e.*, site x month), *L. minutissumum* (433 individuals collected in 153 sampling occasions), *L. malachurum* (188 individuals collected in 111 sampling occasions), *L. mesosclerum* (188 individuals collected in 124 sampling occasions), and *Seladonia subaurata* (188 individuals collected in 110 sampling occasions).

Hoverflies, on the other hand, were much less frequent, with only 277 individuals belonging to 30 species collected (Table 2). The most abundant and common species were *Sphaerophoria scripta* (65 individuals collected in 39 sampling occasions), *Pipizella viduata* (34 individuals collected in 28 sampling occasions) *Episyrphus balteatus* (26 individuals collected in 21 sampling occasions), *Melanostoma mellinum* (23 individuals collected in 14 sampling occasions), and *Eupeodes corollae* (23 individuals collected in 14 sampling occasions).

Table 2: List of pollinator species collected, frequency (number of sampling occasions) and abundance.

Pollinator species	Abundance	Frequency
Wild bees		
Andrena flavipes	27	20
Andrena florea	5	4
Andrena hesperia	1	1
Andrena humilis	10	8
Andrena labiata	1	1
Andrena minutula	15	12
Andrena minutuloides	17	14
Andrena nigroolivacea	7	7
Andrena ovatula	5	5
Andrena sp. 1	1	1
Andrena sp. 2	1	1
Anthidium oblongatum	2	2
Bombus argillaceus	9	9
Bombus pascuorum	30	22
Bombus sylvarum	1	1
Bombus terrestris	21	20
Ceratina cucurbitina	21	15
Ceratina cyanea	10	10
Ceratina dallatorreana	3	3
Dasypoda hirtipes	1	1
Eucera clypeata	2	2
Eucera nigrescens	1	1

Eucera sp.	1	1
Halictus compressus	101	61
Halictus maculatus	29	25
Halictus scabiosae	130	91
Halictus simplex	61	45
Halictus simplex-group	168	105
Hoplitis leucomelana	1	1
Hoplitis papaveris	1	1
Hylaeus annularis	11	11
Hylaeus gibbus	25	23
Hylaeus imparilis	2	1
Hylaeus punctatus	2	2
Hylaeus sp. 1	2	1
Hylaeus sp. 2	1	1
Lasioglossum angusticeps	10	8
Lasioglossum calceatum	3	3
Lasioglossum discum	35	34
Lasioglossum glabriusculum	1,468	305
Lasioglossum leucozonium	57	46
Lasioglossum lucidulum	27	18
Lasioglossum malachurum	188	111
Lasioglossum medinai	124	69
Lasioglossum mesosclerum	188	124
Lasioglossum minutissimum	433	153
Lasioglossum morio	135	78
Lasioglossum nigripes	7	7
Lasioglossum nitidulum	77	11
Lasioglossum pauxillum	165	66
Lasioglossum politum	5	4
Lasioglossum punctatissimum	2	2
Lasioglossum pygmaeum	2	2
Lasioglossum quadrinotatulum	1	1
Lasioglossum villosulum	49	45
Lasioglossum zonulum	80	65
Macropis europaea	2	2
Megachile apicalis	1	1
Megachile centuncularis	1	1
Megachile pilidens	12	12
Nomada sexfasciata	1	1
Nomada sp. 1	1	1
Nomada sp. 2	2	1
Nomiapis diversipes	10	10
Osmia caerulescens	4	4
Seladonia smaragdula	1	1
Seladonia subaurata	188	110
Seladonia tumulorum	8	7
Sphecodes alternatus	2	2
Sphecodes gibbus	4	4

Sphecodes longulus	3	3
Sphecodes puncticeps	1	1
Sphecodes scabricollis	2	2
Sphecodes schenckii	2	2
Stelis breviuscula	1	1
Systropha curvicornis	2	2
Tetralonia salicariae	2	2
Xylocopa violacea	1	1
Hoverflies		
Chrysotoxum bicinctum	1	1
Episyrphus balteatus	26	21
Eristalinus sepulchralis	16	10
Eristalis arbustorum	11	9
Eristalis tenax	17	14
Eumerus funeralis	1	1
Eupeodes corollae	23	14
Eupeodes luniger	2	2
Helophilus pendulus	1	1
Helophilus trivittatus	8	8
Melanostoma mellinum	23	14
Meliscaeva auricollis	1	1
Merodon avidus	1	1
Merodon sp.	1	1
Myathropa florea	2	2
Neoascia podagrica	1	1
Paragus pecchiolii	7	5
Paragus sp.	1	1
Pipiza sp.	1	1
Pipizella sp.	7	6
Pipizella viduata	34	28
Scaeva pyrastri	1	1
Sphaerophoria rueppelli	13	12
Sphaerophoria scripta	65	39
Sphaerophoria sp.	1	1
Syritta pipiens	1	1
Syrphus ribesii	3	2
Syrphus vitripennis	6	4
Xanthandrus comtus	1	1
Xanthogramma pedissequum	1	1

Species accumulation curves showed that sampling completeness was comparable among landscapes, despite variations in the number of sampled sites (Figure 5).

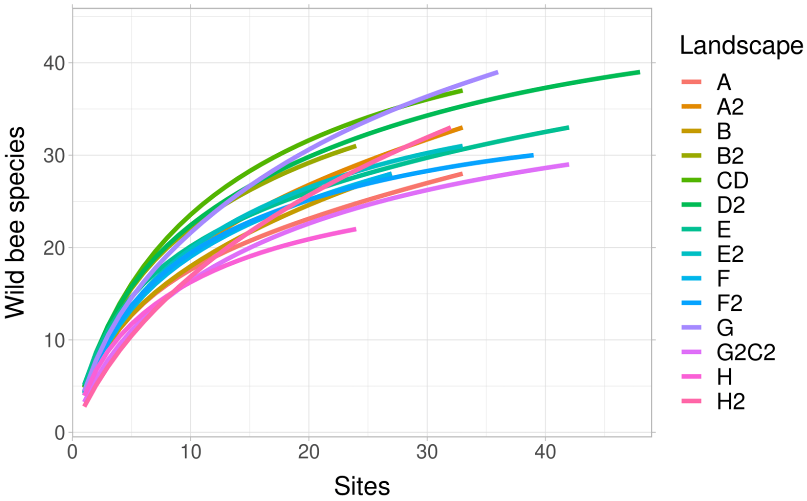

Figure 5: Species accumulation curves for the sampled landscapes. The x-axis represents the number of sampled sites, the y-axis represents the cumulative number of wild bee species collected, and each line represents one of the 14 landscapes.

3.1.2. Habitat type and seasonality

Wild bees were most abundant and diverse in fallows (mean: abundance = 33 ± 17.8, richness = 10.9 ± 4.1; total: abundance = 883, richness = 49), followed by crop field margins (mean: abundance = 32.7 ± 14.9, richness = 10.8 ± 3.9; total: abundance = 1,254, richness = 55), hedgerow sites (mean: abundance = 22.4 ± 13.9, richness = 9.4 ± 3.6; total: abundance = 920, richness = 51), and road verge sites (mean: abundance = 23.9 ± 18.9, richness = 7.4 ± 3.7; total: abundance = 976, richness = 49).

Despite their lower numbers, hoverflies were most frequently collected in hedgerows (mean: abundance = 2.1 ± 2.9, richness = 0.7 ± 1.1; total: abundance = 95, richness = 21), followed by crop field margin sites (mean: abundance = 1.6 ± 1.6, richness = 0.5 ± 0.7; total: abundance = 69, richness = 15), fallow sites (mean: abundance = 1.7 ± 1.6, richness = 0.5 ± 0.9; total: abundance = 51, richness = 15), and road verge sites (mean: abundance = 1.4 ± 1.8, richness = 0.3 ± 0.5; total: abundance = 62, richness = 12).

Most pollinators exhibited generalist habitat use, with species occurring across all habitat types. There were, however, some exceptions, such as the wild bee *Andrena florea* (5 specimens) and the hoverfly *Paragus pecchiolii* (7 specimens), which were collected only in hedgerows. The NMDS analysis of wild bee communities revealed high overlap among habitat types, indicating similar community composition across habitats (Figure 6).

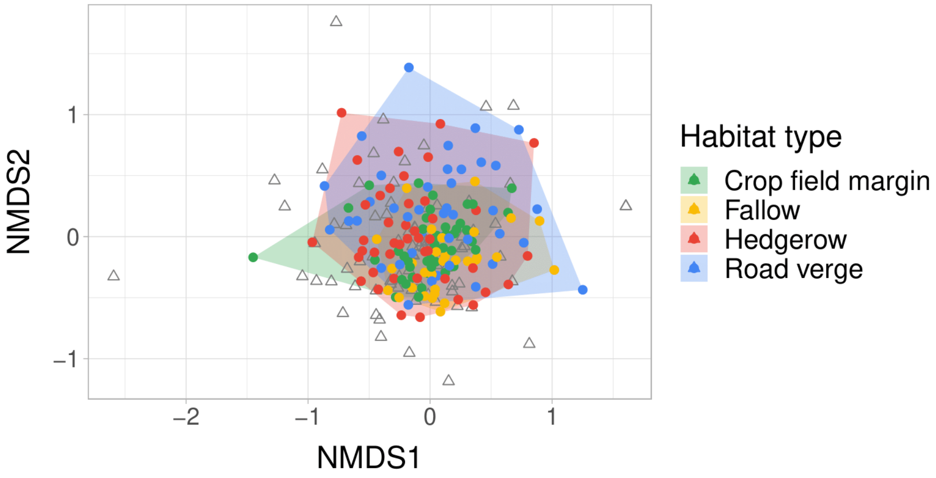

Figure 6: NMDS showing wild bee communities in the four sampled habitat types. Points represent sites, colours represent habitats, and triangles represent wild bee species. The distance between points reflects community dissimilarity, with closer points indicating more similar wild bee species compositions.

We found no interactive effect of habitat type and sampling month on both wild bee abundance and richness (Table 3a, b). However, habitat type had a strong effect on both variables, with both abundance and richness significantly higher in crop field margins and fallows compared to hedgerows and road verges (Table 3a, b, Figure 7).

Similarly, patch centrality was not affected by the interaction between habitat type and sampling month, but it was significantly lower in road verges compared to other habitats (Table 3c, Figure 8). Patch strength, on the other hand, was independent of habitat type (Table 3d).

Table 3: Summary of the linear mixed-effect models testing the effect of the interaction between habitat type and sampling month on a) wild bee abundance (log+10), b) wild bee richness, c) patch centrality, and d) patch strength. The intercept represents crop field margins (habitat type) and May (sampling month). Values in bold indicate significant effects (*p*-value <0.05). Only significant results after a backward stepwise model selection procedure are reported.

	Value	SE	DF	*t*-value	*p*-value
a) Wild bee abundance (log + 10)					
Fallow	-0.011	0.062	141	-0.178	0.859
Hedgerow	-0.176	0.056	141	-3.143	**0.002**
Road verge	-0.163	0.056	141	-2.884	**0.005**
June	0.266	0.037	313	7.260	**<0.001**
July	0.133	0.037	313	3.622	**<0.001**
b) Wild bee richness					
Fallow	-0.055	0.464	141	-0.120	0.905
Hedgerow	-1.033	0.417	141	-2.478	**0.014**
Road verge	-1.567	0.420	141	-3.733	**<0.001**
June	1.532	0.274	313	5.586	**<0.001**

July	1.856	0.275	313	6.757	**<0.001**
c) Patch weighted degree centrality					
Fallow	-0.555	0.560	138	-0.990	0.324
Hedgerow	-0.937	0.499	138	-1.879	0.062
Road verge	-1.035	0.502	138	-2.062	**0.041**
June	4.029	0.455	233	8.860	**<0.001**
July	4.724	0.452	233	10.451	**<0.001**
d) Patch normalized strength					
Fallow	0.004	0.030	141	0.125	0.901
Hedgerow	-0.028	0.026	141	-1.076	0.284
Road verge	-0.049	0.026	141	-1.898	0.060
June	-0.069	0.022	231	-3.134	**0.002**
July	-0.097	0.022	231	-4.315	**<0.001**

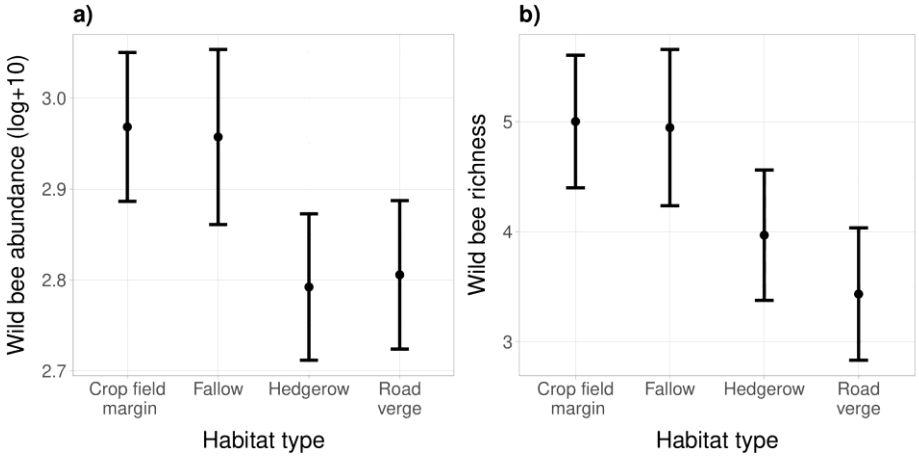

Figure 7: Plots showing the effect of habitat type on a) wild bee abundance (log+10) and b) wild bee richness. Points represent model estimates, and bars represent the 95% confidence intervals.

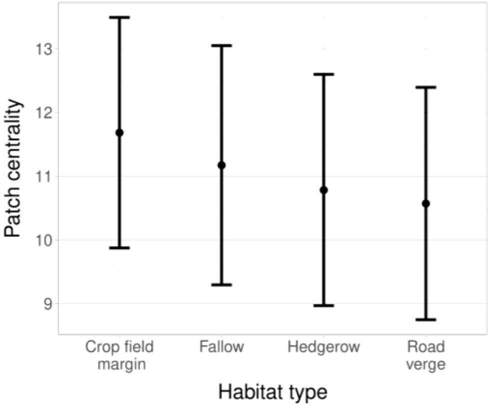

Figure 8: Plot showing the effect of habitat type on patch weighted degree centrality. Points represent model estimates, and bars represent the 95% confidence intervals.

Sampling month strongly affected both wild bee abundance and richness, with a lower number of wild bee specimens and species collected at the beginning of the season (Table 3a, b, Figure 9). In addition, patch weighted degree centrality increased throughout the sampling season, while the effect on patch normalized strength was the opposite (Table 3c, d, Figure 10).

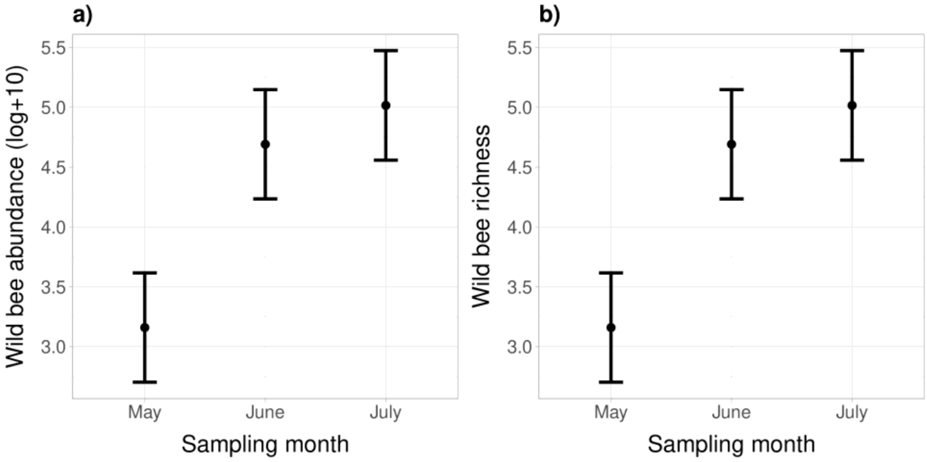

Figure 9: Plots showing the effect of sampling month on a) wild bee abundance (log+10) and b) wild bee richness. Points represent model estimates, and bars represent the 95% confidence intervals.

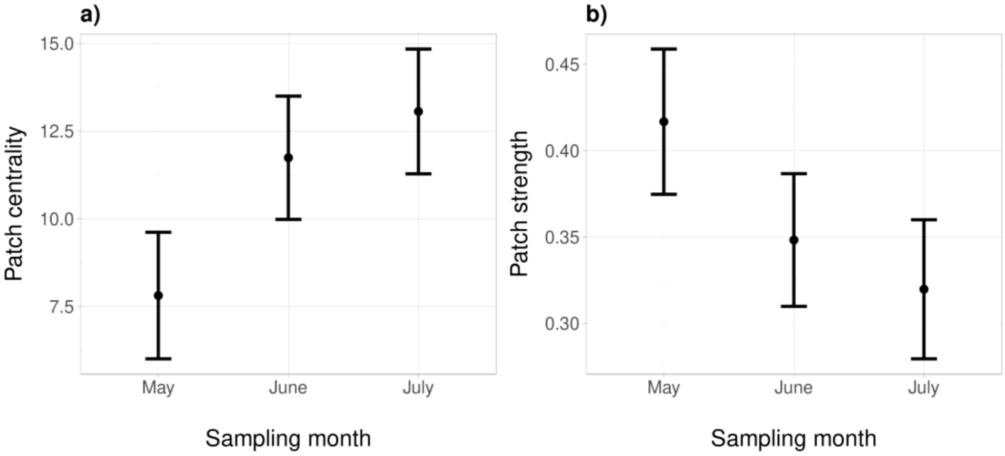

Figure 10: Plots showing the effect of sampling month on a) patch weighted degree centrality and b) patch normalized strength. Points represent model estimates, and bars represent the 95% confidence intervals.

3.1.3. Landscape composition and configuration and seasonality

Landscape composition and configuration had complex effects on network metrics, mediated by seasonality. Network specialization H2' was affected by the interaction between sampling month and the number of crop patches (Table 4a). Specifically, network specialization increased with crop patch numbers only at the beginning of the season (Figure 11a).

Network robustness to patch removal varied depending on the method of removal. When removing first the least-visited patches, robustness was influenced by the interaction between sampling month and the percentage of MFCs in the landscape (Table 4b). In particular, robustness increased with increasing percentage of MFCs only in June, when most MFCs were blooming (Figure 11b). On the other hand, when removing patches in a specific order, robustness was affected by the interaction between sampling month and percentage of semi-natural areas in landscapes (Table 4c). In this case, network robustness strongly decreased with increasing abundance of semi-natural areas only in June (Figure 11c).

Table 4: Summary of the linear mixed-effect models testing the effect of the interactions between the percentage of semi-natural habitat in landscapes and the sampling month, between the percentage of MFCs in landscapes and the sampling month, and between the number of crop patches in landscapes and the sampling month, on a) network specialization (H2', log), b) network robustness to patch removal, calculated by first removing the least-visited patches, and c) network robustness to patch removal, calculated by removing patches in a specific order, based on the probability of habitat loss. The intercept represents May (sampling month). Values in bold indicate significant effects (*p*-value <0.05). Only significant results after a backward stepwise model selection procedure are reported.

	Value	SE	DF	*t*-value	*p*-value
a) Network specialization H2' (log)					
Semi-natural %	0.386	0.539	10	0.717	0.490
Mass-flowering crop %	-0.505	0.459	10	-1.098	0.298
Number of crop patches	0.039	0.016	10	2.471	**0.033**
June	0.517	0.202	19	2.558	**0.019**
July	0.221	0.203	19	1.090	0.289
Number of crop patches × June	-0.051	0.017	19	-3.003	**0.007**
Number of crop patches × July	-0.047	0.017	19	-2.738	**0.013**
b) Network robustness to patch removal (visits)					
Semi-natural %	-0.148	0.102	10	-1.458	0.176
Mass-flowering crop %	0.058	0.154	10	0.375	0.716
Number of crop patches	-0.005	0.002	10	-2.121	0.060
June	-0.098	0.055	19	-1.767	0.093
July	0.008	0.057	19	0.142	0.889
Mass-flowering crop % × June	0.499	0.209	19	2.392	**0.027**
Mass-flowering crop % × July	0.214	0.210	19	1.019	0.321
c) Network robustness to patch removal (habitat)					
Semi-natural %	0.124	0.275	10	0.450	0.662
June	0.159	0.059	19	2.702	**0.014**
July	0.140	0.060	19	2.330	**0.031**
Mass-flowering crop %	0.314	0.161	10	1.954	0.079
Number of crop patches	0.000	0.004	10	0.084	0.935
Semi-natural % × June	-0.605	0.324	19	-1.868	**0.077**
Semi-natural % × July	-0.140	0.343	19	-0.408	0.688

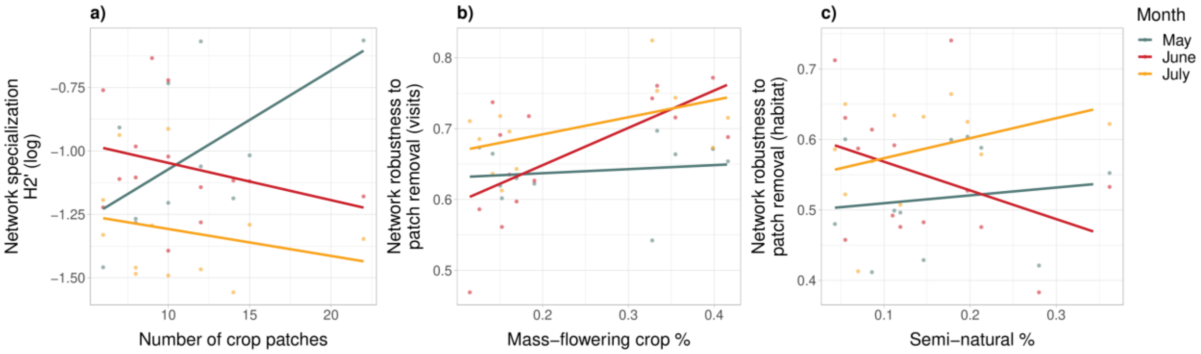

Figure 11: Plots showing the effect of the interaction between sampling month and a) number of crop patches on network specialization (H2', log), b) percentage of MFCs in landscapes on network robustness to patch removal, calculated by first removing the least-visited patches, and c) percentage of semi-natural areas in landscapes on network robustness to patch removal, calculated by removing patches in a specific order, based on the probability of habitat loss. Points represent raw data points and lines represent model estimates.

3.2. Case study 2: Hungary

3.2.1. General results

We collected a total of 165 bee species and 19,911 individuals (Table 5). The most abundant and common species belonged to the Halictidae family, *i.e.*, *Lasioglossum lineare* (3,658 individuals collected in 617 sampling occasions), *L. glabriusculum* (2,350 individuals collected in 534 sampling occasions), *L. pauxillum* (1,722 individuals collected in 631 sampling occasions), *L. leucozonium* (1,425 individuals collected in 577 sampling occasions), and *Halictus simplex* (1,325 individuals collected in 462 sampling occasions).

Table 5: List of bee species collected, frequency (number of sampling occasions) and abundance.

Wild bee species	Abundance	Frequency
Amegilla quadrifasciata	16	13
Andrena bisulcata	1	1
Andrena cordialis	3	3
Andrena curvana	2	2
Andrena flavipes	392	291
Andrena hedikae	1	1
Andrena labialis	1	1
Andrena limata	1	1
Andrena minutuloides	10	9
Andrena nitidiuscula	4	4
Andrena niveata	1	1
Andrena ovatula	10	9
Andrena pallitarsis	1	1

Andrena pilipes	11	10
Andrena ungeri	4	4
Anthidium manicatum	1	1
Anthidium oblongatum	1	1
Anthidium septemspinosum	1	1
Bombus humilis	1	1
Bombus lapidarius	2	2
Bombus muscorum	24	24
Bombus pascuorum	6	6
Bombus sylvarum	25	24
Bombus terrestris	80	72
Ceratina chalcites	1	1
Ceratina chalybea	3	3
Ceratina cyanea	7	7
Coelioxys afer	2	2
Coelioxys brevis	2	2
Coelioxys echinatus	1	1
Coelioxys inermis	1	1
Coelioxys polycentris	2	2
Colletes similis	2	2
Dasypoda hirtipes	120	55
Dasypoda morawitzi	60	50
Epeolus cruciger	2	2
Epeolus variegatus	1	1
Eucera armeniaca	1	1
Eucera clypeata	19	16
Halictus brunnescens	10	4
Halictus compressus	682	321
Halictus langobardicus	132	78
Halictus maculatus	690	376
Halictus patellatus	219	174
Halictus quadricinctus	936	471
Halictus scabiosae	1	1
Halictus sexcinctus	1,161	489
Halictus simplex	1,325	462
Halictus sp.	1	1
Halictus tetrazonius	4	4
Heriades rubicola	6	6
Heriades truncorum	12	12
Hoplitis leucomelana	25	20
Hoplitis tridentata	1	1
Hylaeus angustatus	10	9
Hylaeus annularis	56	50
Hylaeus brevicornis	19	18
Hylaeus communis	8	7
Hylaeus confusus	1	1
Hylaeus cornutus	3	3
Hylaeus gibbus	27	22

Hylaeus gracilicornis	1	1
Hylaeus hyalinatus	5	3
Hylaeus leptocephalus	1	1
Hylaeus lineolatus	2	2
Hylaeus moricei	22	20
Hylaeus pectoralis	41	36
Hylaeus pfankuchi	2	2
Hylaeus styriacus	2	2
Hylaeus trinotatus	1	1
Hylaeus variegatus	3	3
Lasioglossum aeratum	2	2
Lasioglossum albipes	18	13
Lasioglossum bluethgeni	18	13
Lasioglossum brevicorne	4	4
Lasioglossum calceatum	698	392
Lasioglossum clypeare	2	2
Lasioglossum crassepunctatum	101	65
Lasioglossum discum	709	446
Lasioglossum fulvicorne	1	1
Lasioglossum glabriusculum	2,350	534
Lasioglossum griseolum	9	9
Lasioglossum interruptum	52	25
Lasioglossum laterale	3	3
Lasioglossum laticeps	16	15
Lasioglossum lativentre	1	1
Lasioglossum leucozonium	1,425	577
Lasioglossum lineare	3,658	617
Lasioglossum lucidulum	20	16
Lasioglossum majus	1	1
Lasioglossum malachurum	336	82
Lasioglossum mandibulare	192	63
Lasioglossum minutissimum	2	2
Lasioglossum morio	111	81
Lasioglossum nigripes	45	36
Lasioglossum nitidiusculum	1	1
Lasioglossum pauperatum	1	1
Lasioglossum pauxillum	1,722	631
Lasioglossum politum	10	7
Lasioglossum punctatissimum	46	23
Lasioglossum puncticolle	16	14
Lasioglossum pygmaeum	3	3
Lasioglossum semilucens	1	1
Lasioglossum sexnotatum	1	1
Lasioglossum sexstrigatum	2	2
Lasioglossum sp.	2	2
Lasioglossum trichopygum	2	2
Lasioglossum truncaticolle	14	14

Lasioglossum villosulum	238	182
Lasioglossum zonulum	449	309
Lithurgus chrysurus	1	1
Lithurgus cornutus	1	1
Megachile albisecta	2	2
Megachile analis	2	2
Megachile centuncularis	32	31
Megachile deceptoria	20	20
Megachile ericetorum	1	1
Megachile leachella	2	2
Megachile maritima	12	12
Megachile pilidens	17	17
Megachile rotundata	6	6
Megachile versicolor	2	2
Melitta leporina	5	5
Nomada bluethgeni	1	1
Nomada distinguenda	15	14
Nomada fucata	32	29
Nomada rhenana	1	1
Nomada sp.	1	1
Nomiapis bispinosa	4	4
Nomiapis diversipes	23	22
Nomiapis unidentata	1	1
Nomioides minutissimus	3	3
Osmia caerulescens	1	1
Osmia spinulosa	6	6
Panurgus calcaratus	24	22
Rhophitoides canus	10	9
Seladonia confusa	3	3
Seladonia gavarnica	5	5
Seladonia kessleri	55	29
Seladonia pollinosa	18	18
Seladonia seladonia	17	16
Seladonia semitecta	3	3
Seladonia smaragdula	139	106
Seladonia subaurata	690	363
Seladonia tumulorum	3	3
Seladonia vestita	172	118
Sphecodes crassus	2	2
Sphecodes ephippius	3	3
Sphecodes ferruginatus	1	1
Sphecodes gibbus	10	9
Sphecodes intermedius	1	1
Sphecodes miniatus	1	1
Sphecodes monilicornis	8	8
Sphecodes pellucidus	1	1
Sphecodes puncticeps	7	7
Sphecodes rufiventris	2	2

Sphecodes sp.	1	1
Systropha curvicornis	1	1
Tetralonia alticincta	7	7
Tetralonia dentata	9	9
Tetralonia lyncea	1	1
Tetralonia salicariae	7	6
Tetralonia scabiosae	1	1
Triepeolus tristis	1	1
Xylocopa violacea	3	3

Species accumulation curves showed comparable sampling efforts across the 24 landscapes (Figure 12).

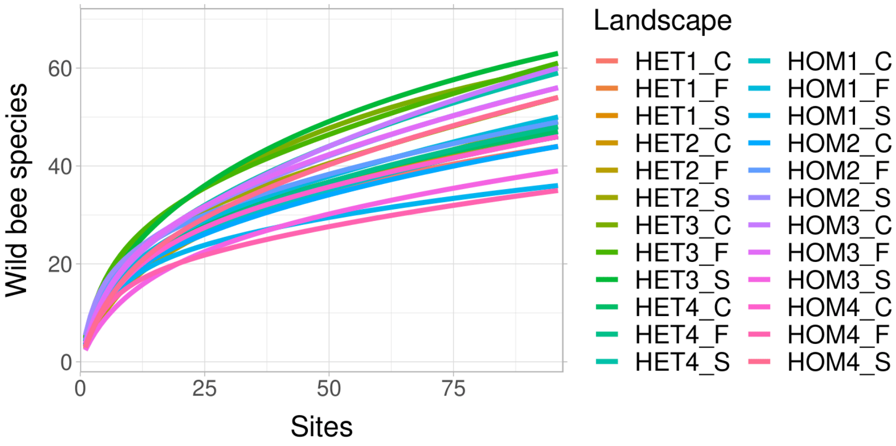

Figure 12: Species accumulation curves for the sampled landscapes. The x-axis represents the number of sampled sites, the y-axis represents the cumulative number of wild bee species collected, and each line represents one of the 24 landscapes.

Regarding flower strips and fields, in the first year, the vegetation was dominated by fast-growing agricultural weeds, which were largely outcompeted in the second year by sown plant species (Figure 13).

Figure 13: Close-ups of the wildflower parcel show the successional development from a) the first year and b) the second year. Photographer: Viktor Szigeti.

3.2.2. Habitat type and inter-annual variation

Wild bees were most abundant and diverse in reed beds (mean: abundance = 43.2 ± 34.7, richness = 13.7 ± 4.5; total: abundance = 2,160, richness = 94), followed by arable lands (mean: abundance = 34.6 ± 26.1, richness = 11.4 ± 3.9; total: abundance = 14,531, richness = 143), road verges (mean: abundance = 38.1 ± 34.5, richness = 11 ± 5.2; total: abundance = 992, richness = 53), and grasslands (mean: abundance = 26.1 ± 18.1, richness = 9.6 ± 3.8; total: abundance = 2,228, richness = 76).

The NMDS analysis showed that the four sampled habitat types hosted similar bee communities (Figure 14).

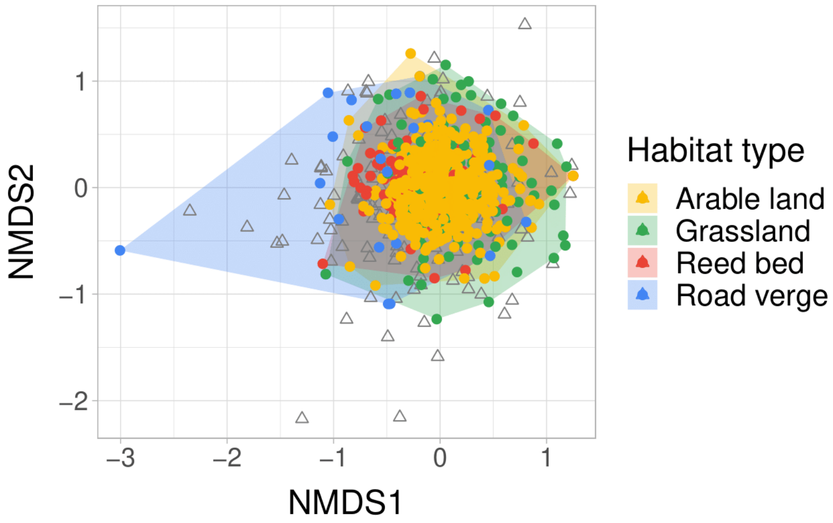

Figure 14: NMDS analysis showing wild bee communities in the four sampled habitat types. Points represent sites, colours represent habitat types, and triangles represent wild bee species. The distance between points reflects community dissimilarity, with closer points indicating more similar wild bee species compositions.

Wild bee abundance and richness were not affected by the interactions between habitat type and sampling year but were influenced by each variable independently (Table 6). Wild bee abundance was lower in grasslands compared to arable land, reed beds, and road verges (Table 6a, Figure 15a). On the other hand, wild bee richness was significantly higher in reed beds compared to all other habitat types (Table 6b, Figure 15b). In addition, both wild bee abundance and richness were significantly higher in 2021 and 2022 compared to 2020 and 2023 (Table 6, Figure 16).

Table 6: Summary of the linear mixed-effect models testing the effect of the interactions between habitat type and the sampling year on a) wild bee abundance (log+1) and b) wild bee richness (log+10). The intercept represents arable land (habitat type) and 2020 (sampling year). Values in bold indicate significant effects (*p*-value <0.05). Only significant results after a backward stepwise model selection procedure are reported.

	Value	SE	DF	*t*-value	*p*-value
a) Wild bee abundance (log+1)					

Grassland	-0.197	0.058	1,722	-3.381	**0.001**
Reed bed	0.136	0.076	1,722	1.794	0.073
Road verge	-0.165	0.101	1,722	-1.629	0.104
2021	1.132	0.053	1,722	21.498	**<0.001**
2022	0.992	0.053	1,722	18.829	**<0.001**
2023	-0.589	0.053	1,722	-11.172	**<0.001**
b) Wild bee richness (log+10)					1,722
Grassland	-0.044	0.012	1,722	-3.689	**<0.001**
Reed bed	0.069	0.015	1,722	4.509	**<0.001**
Road verge	-0.027	0.021	1,722	-1.309	0.191
2021	0.223	0.011	1,722	20.926	**<0.001**
2022	0.253	0.011	1,722	23.721	**<0.001**
2023	-0.098	0.011	1,722	-9.150	**<0.001**

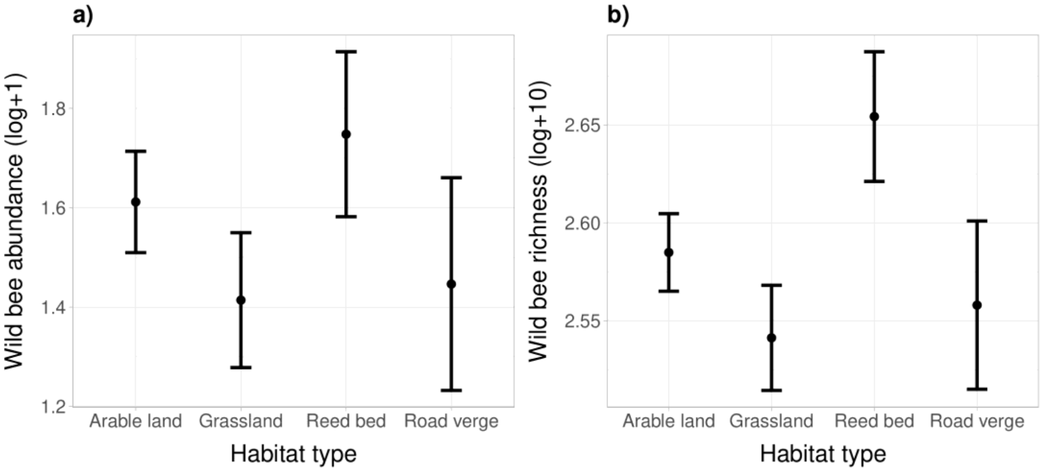

Figure 15: Plots showing the effect of habitat type on a) wild bee abundance (log+1) and b) wild bee richness (log+10). Points represent model estimates, and bars represent the 95% confidence intervals.

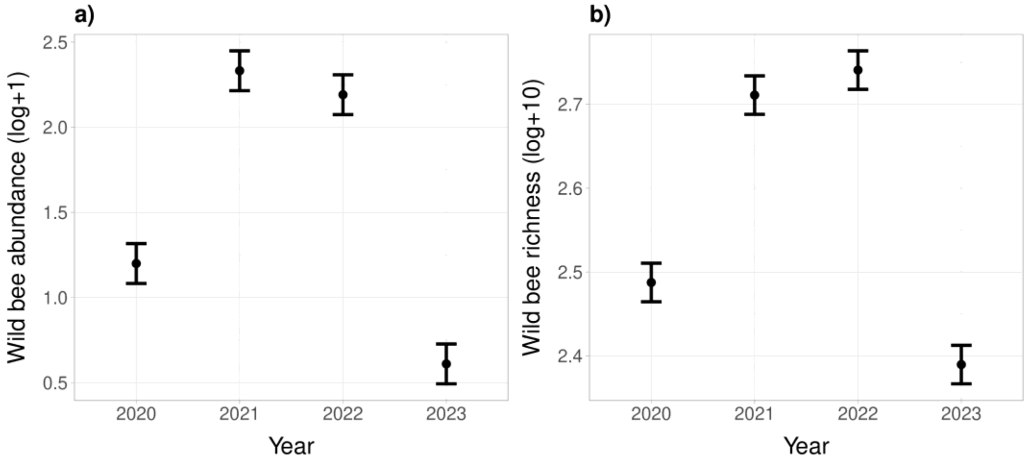

Figure 16: Plots showing the effect of sampling year on a) wild bee abundance (log+1) and b) wild bee richness (log+10). Points represent model estimates, and bars represent the 95% confidence intervals.

Patch weighted degree centrality and normalized strength were affected by the interaction between habitat type and sampling year (Table 7). Patch centrality was similar among habitats in 2020 and 2022, while in 2021 it was significantly higher for reed beds and lower for grasslands, and in 2023, it was significantly higher for arable crops (Figure 17a). Patch strength showed a different trend, with generally lower values in arable crops and grasslands compared to reed beds and road verges, though habitat differences were not evident in 2021 (Figure 17b).

Table 7: Summary of the linear mixed-effect models testing the effect of the interaction between habitat type and sampling year on a) patch centrality and b) patch strength (log). Values in bold indicate significant effects (*p*-value <0.05).

	χ^2	DF	*p*-value
a) Patch weighted degree centrality			
Habitat type	3.186	3	0.364
Year	1016.465	3	**<0.001**
Habitat type × Year	49.289	9	**<0.001**
b) Patch normalized strength (log)			
Habitat type	2.474	3	0.480
Year	94.739	3	**<0.001**
Habitat type × Year	32.641	9	**<0.001**

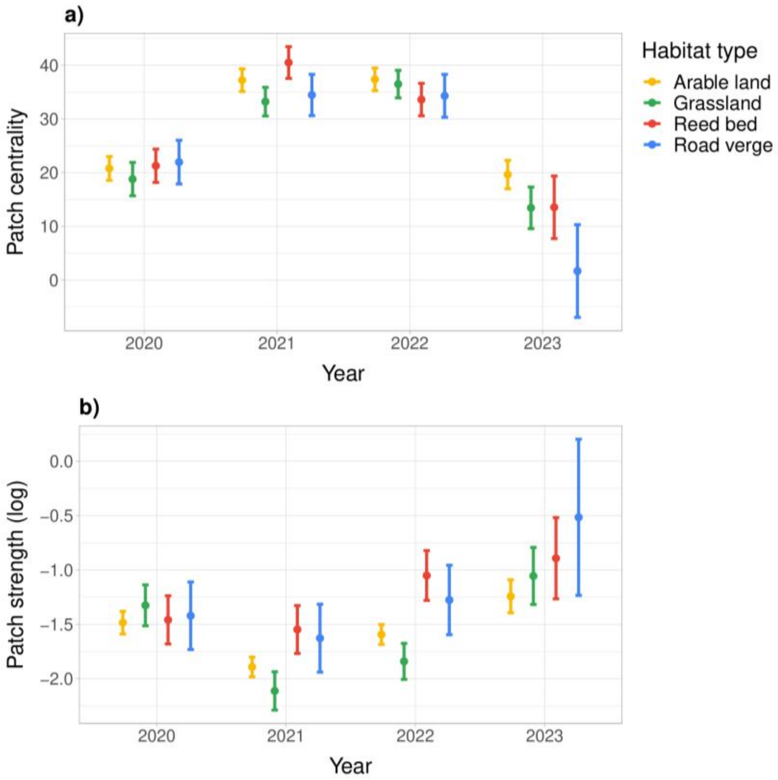

Figure 17: Plots showing the effect of the interaction between habitat type and sampling year on a) patch weighted degree centrality and b) patch normalized strength (log). Colours represent habitat types, points represent model estimates, and bars represent the 95% confidence intervals.

3.2.3. Pollinator-friendly interventions and inter-annual variation

Distance from pollinator-friendly interventions (flower strip or flower field) significantly affected wild bee abundance and richness, with both metrics higher at sites closer to the intervention (Table 8, Figure 18). However, distance did not influence patch centrality or strength (Table 8).

Table 8: Summary of the linear mixed-effect models testing the effect of the interaction between distance from pollinator-friendly interventions in landscapes and sampling year on a) wild bee abundance (log+1), b) wild bee richness (log+10), c) patch weighted degree centrality, and d) patch normalized strength (log). The intercept represents distance from pollinator-friendly intervention = 1 and 2020 (sampling year). Values in bold indicate significant effects (*p*-value <0.05). Only significant results after a backward stepwise model selection procedure are reported.

	Value	SE	DF	*t*-value	*p*-value
a) Wild bee abundance (log+1)					
Distance = 2	-0.084	0.070	365	-1.192	0.234
Distance = 3	-0.161	0.081	365	-1.981	**0.048**
Distance = 4	-0.122	0.070	365	-1.732	0.084
2021	1.074	0.066	1,149	16.200	**<0.001**
2022	1.062	0.066	1,149	16.020	**<0.001**
2023	-0.543	0.066	1,149	-8.186	**<0.001**
b) Wild bee richness (log+10)					
Distance = 2	-0.013	0.014	365	-0.935	0.350
Distance = 3	-0.037	0.016	365	-2.256	**0.025**
Distance = 4	-0.021	0.014	365	-1.519	0.130
2021	0.224	0.013	1,149	16.769	**<0.001**
2022	0.270	0.013	1,149	20.228	**<0.001**
2023	-0.093	0.013	1,149	-6.945	**<0.001**
c) Patch weighted degree centrality					
Distance = 2	-0.607	0.725	358	-0.837	0.403
Distance = 3	-0.321	0.858	358	-0.374	0.708
Distance = 4	-0.744	0.726	358	-1.024	0.306
2021	15.586	0.693	539	22.496	**<0.001**
2022	17.805	0.689	539	25.824	**<0.001**
2023	1.238	1.112	539	1.113	0.266
d) Patch normalized strength (log)					
Distance = 2	-0.607	0.725	358	-0.837	0.403
Distance = 3	-0.321	0.858	358	-0.374	0.708
Distance = 4	-0.744	0.726	358	-1.024	0.306
2021	15.586	0.693	539	22.496	**<0.001**
2022	17.805	0.689	539	25.824	**<0.001**
2023	1.238	1.112	539	1.113	0.266

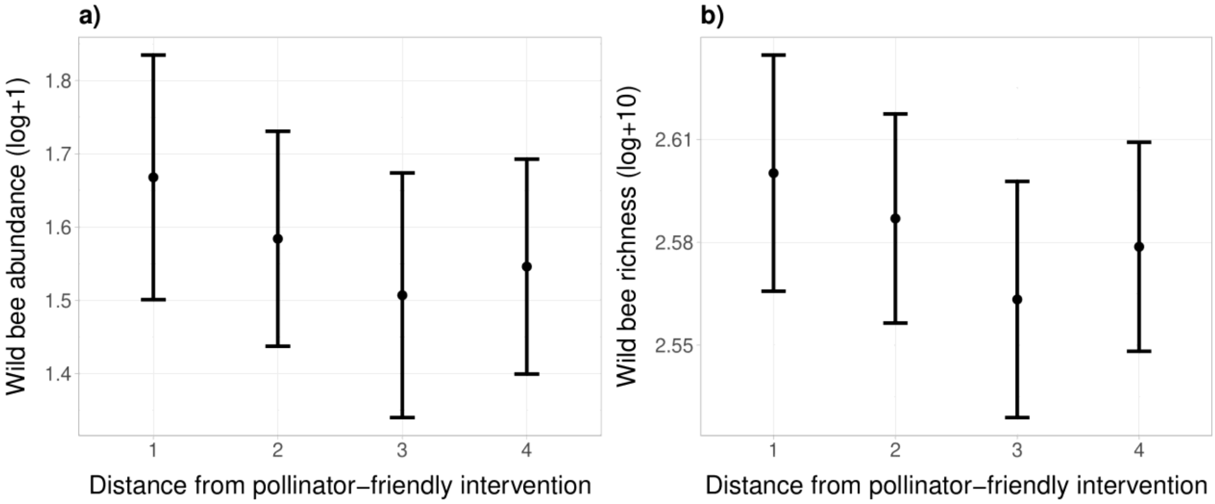

Figure 18: Plots showing the effect of distance from pollinator-friendly intervention (flower field or flower strips) on a) wild bee abundance (log+1) and b) wild bee richness (log+10). Points represent model estimates, and bars represent the 95% confidence intervals.

3.2.4. Landscape composition and inter-annual variation

We found no effect of intervention type and landscape type on network metrics (Table 9). Sampling year, on the other hand, strongly affected all indices. Network specialization was higher in 2020 and 2023 compared to 2021 and 2022 (Figure 19a), while network robustness to patch removal calculated with both methods was significantly higher in 2021 (Figure 19b, c).

Table 9: Effect of the interaction between intervention type and sampling year, between landscape type and sampling year, and between intervention type and landscape type on a) network specialization (H2’, log), b) network robustness to patch removal, calculated by first removing the least-visited patches, and c) network robustness to patch removal, calculated by removing patches in a specific order, based on the probability of habitat loss. The intercept represents control sites (pollinator-friendly intervention type, landscapes with no pollinator-friendly interventions), heterogeneous landscapes (landscape type), and 2020 (sampling year). Values in bold indicate significant effects (*p*-value <0.05). Only significant results after a backward stepwise model selection procedure are reported.

	Value	SE	DF	*t*-value	*p*-value
a) Network specialization H2’ (log)					
Flower field	0.038	0.072	20	0.525	0.606
Flower strips	0.024	0.070	20	0.343	0.735
Homogeneous landscape	-0.041	0.058	20	-0.716	0.483
2021	-0.146	0.065	50	-2.239	**0.030**
2022	-0.205	0.065	50	-3.149	**0.003**
2023	0.010	0.088	50	0.108	0.914

b) Network robustness to patch removal (visits)					
Flower field	-0.019	0.018	20	-1.031	0.315
Flower strips	-0.019	0.018	20	-1.074	0.296
Homogeneous landscape	-0.002	0.015	20	-0.170	0.867
2021	0.055	0.016	50	3.390	**0.001**
2022	0.014	0.016	50	0.852	0.398
2023	-0.036	0.022	50	-1.651	0.105
c) Network robustness to patch removal (habitat)					
Flower field	0.009	0.027	20	0.321	0.752
Flower strips	-0.002	0.026	20	-0.061	0.952
Homogeneous landscape	0.012	0.022	20	0.548	0.590
2021	0.062	0.019	50	3.227	**0.002**
2022	0.007	0.019	50	0.367	0.715
2023	-0.010	0.026	50	-0.367	0.715

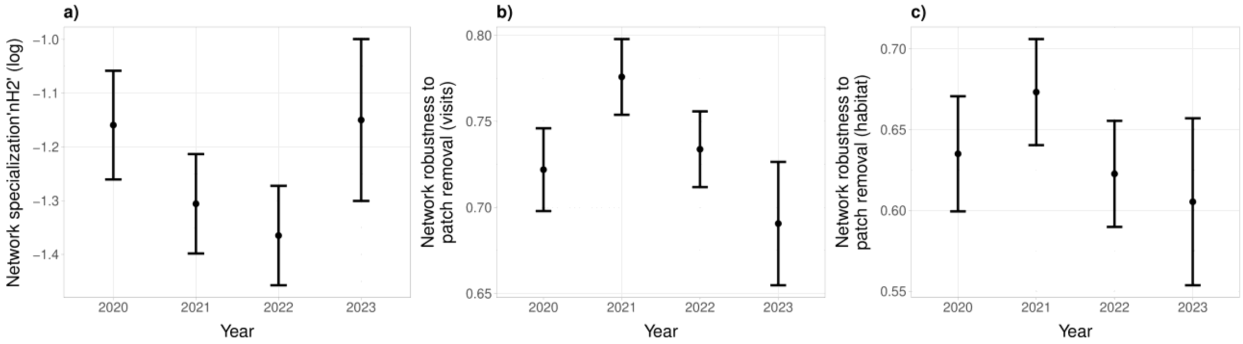

Figure 19: Plots showing the effect of sampling year on a) network specialization (H2', log), b) network robustness to patch removal, calculated by first removing the least-visited patches, and c) network robustness to patch removal, calculated by removing patches in a specific order, based on the probability of habitat loss. Points represent model estimates, and bars represent the 95% confidence intervals.

4. Discussion

In this deliverable, we investigated the role of different habitat types and pollinator-friendly interventions on wild pollinators in supporting wild pollinator communities in agricultural landscapes. The findings from both case studies confirmed that overall pollinator communities were similar across habitats. Landscape composition and configuration, as well as seasonal and inter-annual variability, further modulated these effects. Understanding these dynamics is essential for developing effective conservation strategies to sustain pollinators within agricultural ecosystems. Our results will contribute to developing effective landscape planning strategies to support pollinators in intensive landscapes. The most surprising result of both study cases is that when multiple habitats are sampled across a single landscape, bees are able to use all the habitats irrespective of their quality and structure.

4.1. Habitat type

In the Italian case study, we observed that fallows and crop field margins supported significantly higher wild bee abundance and richness compared to hedgerows and road verges, emphasizing the value of open habitats in providing essential resources for pollinators. On the other hand, in the Hungarian case study, pollinator richness was higher in reed beds, while arable lands supported the highest abundance of wild bees. These results suggest that despite intensive agricultural practices, specific agricultural habitats can still provide valuable resources for pollinators, therefore, maintaining heterogeneous landscapes with a mix of semi-natural and cultivated habitats can enhance pollinator conservation efforts (Eeraerts et al. 2021). The role of reed beds in pollinator support is particularly noteworthy, as these habitats are often overlooked in conservation strategies but may offer nesting sites and floral resources for a diverse range of pollinator species. While limited studies have explored wild pollinator communities in wetlands and in particular in reed beds, existing research highlights their importance in supporting wild bees and wasps (Heneberg et al. 2014; Bogusch et al. 2020). Reed beds are especially crucial for specialized species nesting in cavities, such as the colletid bee *Hylaeus pectoralis*, of which we collected 41 specimens, and which utilizes cigar galls formed by the frit fly *Lipara lucens* on common reed stems (Bogusch et al. 2024). In contrast, road verges emerged as the least suitable habitats for wild bees in both studies, likely due to a combination of low floral resources and high levels of disturbance and pollution. Vajna et al. (2024) also found in the Hungarian study area, that road verges are avoided by pollinators, compared to more flower-rich habitats. Roads expose pollinators to various pollutants, including light, noise, exhaust fumes, and heavy metals, and may act as barriers to pollinator movement (Greenleaf et al. 2007; Girling et al. 2013; Dargas et al. 2016; Phillips et al. 2020). Given the extensive area that they cover, we recommend revised management approaches that promote increased floral resources in these areas, as also suggested by other studies (Baldock et al. 2019; Phillips et al. 2020).

Despite significant differences in wild pollinator abundance and richness among habitat types, the NMDS analysis revealed a strong overlap among wild bee communities across different habitats. This suggests that wild bees in agricultural landscapes are weakly associated with single habitat types, with most species interacting with multiple habitats in landscapes, and advocating the equivalent role of habitats across landscapes for wild bees, in contrast with previous studies that emphasize the complementary nature of multiple habitats in sustaining wild bees in agricultural landscapes (*e.g.*, Proesmans et al. 2019b; Maurer et al. 2022). Our results might be explained by the fact that agricultural intensification may select for generalist wild bees, in terms of habitat preferences, acting as a filter (Gámez-Virués et al. 2015; Ockermüller et al. 2023), similar to what happens in urban landscapes (Geppert et al. 2025). For instance, intensive landscapes are less favourable for bumblebee species with above-ground nests, small colonies, and long colony cycles, indicating that both nesting habitat and the spatiotemporal availability of food resources serve as ecological filters for these key pollinators (Persson et al. 2015). Simplified pollinator communities in agricultural landscapes can also lead to reduced crop yield and quality (Grab et al. 2019). This result is central, as it emphasizes the importance of considering the entire landscape in conservation strategies for wild bees rather than focusing on single habitat patches.

As most habitat types held similar importance across landscapes, we highlighted mixed effects of habitat type on both patch centrality and strength. In the Italian case study, patch strength was not influenced by habitat type, and patch centrality was comparable among crop field margins, fallows, and hedgerows, with lower values in road verges. These results suggest the absence of key patches in landscapes, playing a fundamental role in supporting pollinator species across entire networks. The most peripheral nodes, *i.e.*, those showing low centrality values, were represented by road verges. A low centrality value could indicate a patch hosting few wild bee species or specialist species. In our study, the low centrality values of road verges were related to low species richness, as the NMDS analysis did not highlight the presence of specialist species in road verges. Again, our result is related to the fact that wild bees dynamically use different habitats to meet their resource needs throughout the season (Cole et al. 2017). On the other hand, in the Hungarian case study, the effect of habitat type on patch centrality and strength was complex and mediated by the sampling year; note that there were significant differences in precipitation among years. For example, in 2020 both patch centrality and strength were comparable across all habitat types, similar to the Italian case study. However, in 2021 centrality was higher for arable land and reed bed, and strength was higher for reed bed and road verge. These results indicate that the relative importance of habitats for wild bees is not stable inter-annually and can shift across years, suggesting that specific habitat types may gain importance in certain years due to multiple factors. Analysing patch centrality and strength, while also considering temporal dynamics, can be a useful tool to identify focal patches within a heterogeneous landscape, thereby enhancing conservation planning.

4.2. Pollinator-friendly interventions

In both case studies, we investigated the impact of multiple pollinator-friendly interventions in agricultural landscapes on wild bees measuring their effect at the landscape scale by using a specie-habitat network approach.

In the Italian case study, we focused on permanent interventions, *i.e.*, hedgerows. Contrary to our expectations, we found that wild bee abundance and richness were generally low in this habitat, despite the common perception that hedgerows provide valuable resources for wild pollinators, including bees (Kremen et al. 2019). This unexpected result highlights the role of hedgerow characteristics such as floral composition, structure and management, in determining their effectiveness. For example, when floral cover of hedgerows is not higher than in other habitats, their positive impact on pollinators becomes less evident (Bishop et al. 2023). Furthermore, existing research suggests that hedgerows are often less effective than other interventions in supporting wild pollinators (von Königslöw et al. 2022). In addition, despite the limited numbers of hoverflies collected, hedgerows appeared to play a crucial role in supporting these pollinators. Their structural complexity, availability of shelter, and potential food sources likely facilitated hoverfly presence, aligning with findings from previous studies (Alison et al. 2022). While hedgerows may not have significantly boosted wild bee populations in our study, their role in agricultural landscapes should not be underestimated, as they can also function as movement corridors, guiding pollinators such as bumblebees and enhancing their ability to navigate fragmented agricultural landscapes (Cranmer et al. 2012).

In the Hungarian case study, we focused on the role of flower strips and fields in supporting wild pollinators. Interestingly, we found that both wild bee abundance and richness declined with increasing distance from the pollinator-friendly interventions, suggesting that the spatial arrangement is a key factor influencing their effectiveness. Many studies highlight the importance of distributing small interventions across landscapes (*e.g.*, Donkersley et al. 2023), and our findings reinforce the necessity of maintaining a network of interconnected pollinator-friendly habitats. Similar results were observed in other studies, where strawberry crops near wildflower strips exhibited higher wild bee visitation rates compared to more distant crops (Ganser et al. 2018). Although flower strips are widely recognized for their strong positive influence on wild pollinator communities (Albrecht et al. 2020; Ganser et al. 2021; von Königslöw et al. 2022), this effect was not evident in our study. This could be related to multiple factors, such as the concentration effect, *i.e.*, pollinators tended to remain in flower strips, which were not sampled in our study, and the size of the flower strips (Krimmer et al. 2019). Overall, these results further underscore the importance of maintaining semi-natural habitats in agricultural landscapes, which often provide more stable and long-term benefits to pollinators than flower strips and need less management (von Königslöw et al. 2021).

Pollinator conservation strategies in agricultural landscapes should therefore extend beyond the establishment of flower strips and focus equally on the management of existing habitats, as the presence of flower strips alone in intensive landscapes is often insufficient to efficiently support pollinators (Mota et al. 2022).

4.3. Temporal variability

While the effect on wild bees of local variables, such as habitat type and pollinator-friendly interventions, exhibited a non-linear pattern, our findings reveal that temporal variation had a strong effect in both case studies.

The Italian case study was conducted over a single season, with wild pollinators sampled three times between May and July. We found a clear temporal trend, with wild bee abundance and richness being significantly lower at the beginning of the season and peaking in June, similar to other studies (Tucker and Rehan 2018). The peak in wild pollinator activity overlapped with the peak flowering of many plant species in the sampling area, as well as the blooming of multiple MFCs, including sunflower, a key MFC in the sampled landscapes. Seasonal changes are known to strongly affect wild pollinators (Turley et al. 2022), and the observed trend aligns with previous studies demonstrating that pollinator dynamic closely tracks floral resource availability (Burkle and Alarcón 2011; CaraDonna et al. 2017; Guezen and Forrest 2021). Conversely, a few studies reported the opposite trend, suggesting that in flower-rich environments, pan trap captures tend to be lower, potentially due to pollinator preference for natural floral resources over artificial traps (Kuhlman et al. 2021). The temporal shift in wild bee abundance and richness also reflects a temporal shift in both patch centrality and strength. In fact, patch centrality increased as the season progressed, while patch strength showed the opposite trend. This suggests that wild bees became more generalized in their habitat use over time, probably as an adaptive response to fluctuating floral resources and floral dearth at the beginning of the season. Such behavioural flexibility may enable pollinators to optimize foraging efficiency in dynamic environments.

In the Hungarian case study, we sampled wild bees for four consecutive years, once per year, at the seasonal peak in July. This long-term dataset revealed significant inter-annual fluctuations in wild bee abundance and richness, with peaks recorded in 2021 and 2022. These variations also influenced species-habitat network properties, resulting in networks that were, on average, less specialized and more robust in 2021 and 2022. This variability may be attributed to a combination of climatic factors, such as fluctuations in temperature and precipitation, as well as the role in the landscape of the ecological succession in managed flower strips, which have been shown to become more attractive in their early years (Krimmer et al. 2019; Albrecht et al. 2021). Similar inter-annual patterns in pollinator populations have been documented in long-term studies, underscoring the complexity of factors influencing these communities (Kammerer et al. 2021). The observed inter-annual variability highlights the need for long-term monitoring programs to accurately assess pollinator responses to multiple factors, as short-term studies may fail to capture the full range of temporal fluctuations, leading to an incomplete understanding of the effectiveness of conservation measures.

4.4. Landscape composition and configuration

The species-habitat network analysis provided valuable insights into how wild bees use habitat resources at the landscape level, shedding light on the spatial dynamics of their foraging behaviour.

Landscape composition only partially influenced the properties of species-habitat networks. In fact, in the Hungarian case study, we observed no significant effect of landscape heterogeneity on network specialization and robustness to patch removal. This suggests that, in particular contexts, wild bees exhibit a relatively weak response to habitat composition compared to other pollinator guilds (Lami et al. 2021; Fijen et al. 2025). Therefore, the exclusive focus of our work on this pollinator group in our study may have contributed to the observed effect. These results may be also partially explained by the spatial scale considered, as bees often respond to habitat factors at larger scales, up to 10 km (Hellwig et al. 2022). Last, additional local factors may have a dominant role in shaping wild bee communities and their foraging behaviour compared to landscape factors (Schubert et al. 2022; Bishop et al. 2023).

In the Italian case study, on the other hand, we found that the effect of landscape composition on network specialization and robustness to patch removal was modulated by seasonality. Specifically, network specialization strongly increased with increasing number of crop patches in May, while it was independent of landscape context in June and July. Higher floral richness generally enhances network specialization, as pollinators can focus on a narrower subset of plants when resources are abundant (Gómez-Martínez et al. 2022). In our study, at the beginning of the season, when floral resources were relatively scarce, landscapes with small, diverse crop patches probably provided diverse floral resources, therefore increasing pollinator specialization for habitats and general network specialization. Network robustness to patch removal was generally high, as different habitat types provided similar functions. Network robustness was affected by different landscape features, depending on the methodology used for robustness calculation. In particular, network robustness to patch removal calculated by removing first the least-visited patches was constant in May and July, but in June it increased with increasing MFC percentage. On the other hand, network robustness to patch removal calculated by removing patches based on the habitat type was constant in May and July, and decreased with increasing semi-natural percentage in June. This pattern suggests that key MFCs, such as sunflowers, which bloomed in June within our study area, played a key role in shaping pollinator foraging behaviour (Holzschuh et al. 2016). In addition, these results highlight the critical importance of carefully selecting methodological approaches when assessing network robustness, as different calculation methods may yield contrasting outcomes. Overall, our findings suggest that while semi-natural habitats and MFCs provide critical resources for pollinators, they may also create dependencies that reduce network robustness when these habitats are lost (Marini et al. 2019).

5. Conclusion and management recommendations

Through the two case studies, we demonstrated that wild bees exploit agricultural landscapes at a broad scale, showing no strong preference for specific habitat types. This likely results from a filtering effect linked to the relatively high degree of landscape intensification in both regions, which favours a regional pool of species capable of foraging across entire landscapes (Figure 20). Additionally, our results emphasize the dynamic nature of pollinator communities, where temporal variability, both seasonal and inter-annual, plays a crucial role.

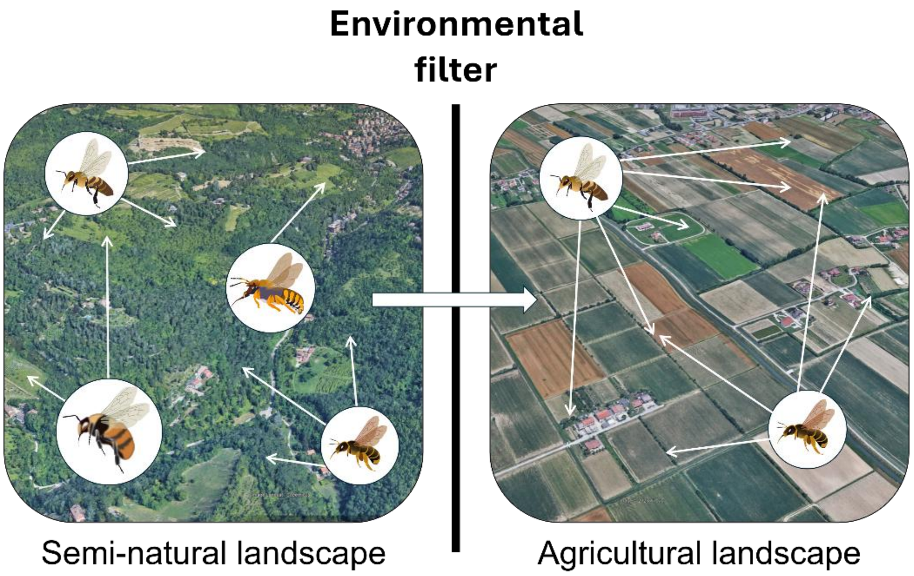

Figure 20: Agricultural intensification acts as a filter for wild bees.

Based on our findings, we highlight the need for a landscape-scale approach to pollinator conservation, and we propose several management recommendations to optimize pollinator conservation in agricultural landscapes:

1. Enhance landscape heterogeneity: while habitats across the landscape were redundant in terms of species composition, specific habitat types, in particular open semi-natural habitats, supported higher wild bee abundance and richness. These habitats should be prioritized in conservation efforts to maximize their benefits for pollinators. In particular, we did not measure the nesting potential of different habitats which probably support the large majority of the species populations that we sampled as adults across all the habitats.
2. Explore the role of overlooked habitats in pollinator conservation: reed beds emerged as promising habitats for wild bees. These habitats remain understudied and should be further investigated to better understand their potential contribution to pollinator conservation.
3. Improve the management of road verges: road verges emerged as the least beneficial habitat for wild bees in both studies. Given their extensive coverage across landscapes, management practices should be revised to better support pollinator populations, for example by reducing the frequency of mowing. However, potential risks such as pollution exposure should also be considered.
4. Optimize management of pollinator-friendly interventions: while flower fields and strips and hedgerows are commonly implemented as pollinator-friendly interventions, their short-term effect on wild bee conservation in our studies appeared to be marginal. These effects could be related to the sampling technique, as well as the flower mix used for flower strips or the floral availability of hedgerows. Both interventions should be always carefully evaluated, for example by strategically placing them to maximize their effectiveness, as their positive effects on wild bees are not straightforward.
5. Consider seasonal and annual variability: the importance of specific habitat types for pollinators varied throughout the season and years, highlighting the need to incorporate temporal variability in pollinator conservation strategies. Long-term monitoring, in particular, is crucial for supporting pollinator populations in dynamic landscapes. In this
6. Consider multiple pollinator guilds: in both studies, we focused on wild bees. However, different pollinator guilds, such as hoverflies and butterflies, could exhibit different responses to environmental factors. Whenever possible, conservation strategies should consider the needs of multiple pollinator guilds to ensure a more comprehensive approach to pollinator conservation.

7. Integrate species-habitat network analysis: network analysis showed that at the landscape level, wild bees act as generalists, visiting multiple habitat types without a strong preference for specific patches. In fact, both patch centrality and strength analysis highlighted that no specific patch showed higher importance for wild bees. The resulting species-habitat network was robust against habitat loss, indicating that current wild bee communities in agricultural landscapes were resilient to specific environmental pressures. Incorporating species-habitat network analysis into conservation planning can provide valuable insights into habitat connectivity and pollinator community resilience.

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