



Does pollinator conservation promote environmental co-benefits?

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ABSTRACT

The decline of pollinators is an urgent issue that has gained global attention and many initiatives have been implemented to promote conservation actions. However, interventions aimed at safeguarding pollinators can have ripple effects on multiple ecosystem services that are equally important for human well-being. In this work, we investigated whether environmental conditions favouring pollinators are positively associated with the provision of multiple ecosystem services across three different habitats. We selected 96 sites belonging to three habitat types with different roles in supporting pollinators, *i.e.*, crop field margins, semi-natural patches, and urban green areas. We sampled wild pollinators and seven ecosystem services, which included provisioning, cultural, and regulatory services, using which we calculated two ecosystem multi-functionality metrics. Semi-natural patches and crop field margins exhibited both the highest diversity of pollinators and ecosystem multi-functionality, *i.e.*, habitats that supported pollinators also delivered a higher number of environmental co-benefits. However, increasing habitat quality for pollinators did not result in increased multi-functionality, indicating that single ESs exhibited non-linear responses. Therefore, improving local conditions for wild pollinators did not enhance ecosystem multi-functionality, while specific habitat types have been shown to have the potential to improve pollinator diversity while generating multiple environmental co-benefits.

1. Introduction

Pollination is one of the most valuable ecosystem services (ESs), with an estimated overall monetary value of about US\$195 billion (Bauer and Sue Wing, 2016). Animal pollination, in particular, is essential for ensuring wild plant reproduction (Aguilar et al., 2006; Ollerton et al., 2011) and maintaining crop productivity (Garibaldi et al., 2014; Klein et al., 2007). Since the decline of pollinators could strongly impact pollination (Reilly et al., 2020), maintaining or increasing pollinator diversity and abundance has become a central target in biodiversity conservation (Brittain et al., 2013; Hallmann et al., 2017; Lemanski et al., 2022). Common interventions to support pollinators include management actions at the local scale, *e.g.*, improving habitat quality by increasing flower cover and diversity (Gill et al., 2016; Klaus et al., 2021; Sutter et al., 2017), but also the enhancement of landscapes, *e.g.*, by restoring natural and semi-natural habitats (Scheper et al., 2013; Tonietto and Larkin, 2018). However, any intervention designed for

pollinators should be carefully assessed, as it could affect multiple ESs both positively and negatively (Galler et al., 2015).

In the best-case scenario, habitat or landscape manipulations to boost pollinator diversity also increase multiple ESs, leading to enhanced ecosystem multi-functionality (EMF). EMF is the capacity of a landscape, habitat, or ecosystem to provide multiple functions at the same time, implying social, economic, and ecological benefits (Byrnes et al., 2014). Until now, most studies on EMF have focused on its association with biodiversity, highlighting positive relationships between EMF and above- and below-ground diversity (Delgado-Baquerizo et al., 2020; Fan et al., 2023; Lefcheck et al., 2015; Maestre et al., 2012; Mensah et al., 2020, but see Gamfeldt and Roger, 2017). A key research gap concerns the response of EMF to conservation actions in different habitat types. In particular, it is not known yet the extent to which management actions designed to conserve pollinators in different environments will lead to positive effects on other ESs, potentially generating environmental co-benefits.

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ES provision worldwide strongly depends on land use change (Gomes et al., 2020; Haddad et al., 2015; Millennium Ecosystem Assessment, 2005). In general, habitats with a favourable conservation status enhance both regulating and cultural ESs (Maes et al., 2012), and a high amount of semi-natural areas enhances biodiversity-based ESs compared to urban and agricultural areas (Baral et al., 2014). For example, pest control is strongly related to the presence of semi-natural habitats in the landscape (Holland et al., 2016; Rega et al., 2018; Rusch et al., 2016), and pollinator diversity declines with increasing distance from semi-natural areas (Ricketts et al., 2008). However, even urban areas, especially those characterized by a moderate level of urbanization and rich in green areas, seem to better support pollinators and the ESs they provide than agricultural areas (Theodorou et al., 2020; Wenzel et al., 2020, but see Baldock et al., 2015). Usually, agricultural areas are fundamental for crop production but are poor in delivering other ESs, particularly regulating ones (Laura et al., 2017; Maes et al., 2012; Tóth et al., 2018). Nonetheless, most of these studies analysed how single ES provisioning changed in different habitat types, without taking into account the possible interactions among ESs.

In this work, we measured wild pollinator diversity, flower cover and diversity and seven ESs, comprising provisioning, regulating and cultural ESs, through eight ES indicators. We selected 96 sampling sites in north-eastern Italy belonging to three habitat types, *i.e.*, crop field margins, semi-natural patches, and urban green areas. Selected habitats represent common land-use categories, each potentially suitable to support pollinators but characterised by a distinct degree of relevance to pollinators. Moreover, sites belonging to the same habitat were selected along a gradient of habitat quality for pollinators, estimated through flower cover and diversity. Our specific aims were 1) to understand how wild pollinator diversity and EMF varied among different habitat types, and 2) to test whether improving local conditions for pollinators would also boost EMF. We expect that both pollinator diversity and EMF would be higher in semi-natural patches and that EMF would increase with increasing flower cover and diversity, suggesting that both restoring semi-natural habitats and improving existing habitat quality for pollinators should produce multiple environmental co-benefits.

2. Materials and methods

2.1. Study area and sampling design

We selected four regions in north-eastern Italy (Table S1, Fig. S1). Within each region, we selected 24 sampling sites representing three habitat types: crop field margins, which included simple herbaceous margins and complex margins; semi-natural patches, which included grasslands and open abandoned areas; and urban green areas, which included both private and public gardens. Within each region, we selected 8 sites for each habitat type. Within each habitat, sites were chosen *a priori* along a gradient of quality for pollinators, taking into account both the cover and diversity of floral resources. Sites belonging to the same habitat type were at least 500 m away from each other. Climatic conditions of sites were similar since elevation ranged between 10 and 550 m above sea level. Minimum annual temperatures ranged from 0 °C in January and 18 °C in July, maximum annual temperatures ranged from 6 °C in January and over 30 °C in July, and total annual precipitation ranged from 800 to 1100 mm.

2.2. Wild pollinator and plant sampling

We sampled wild pollinators, *i.e.*, wild bees (Hymenoptera: Apoidea: Anthophila) and hoverflies (Diptera: Syrphidae), using pan traps. At each site, we placed three pan traps (yellow, blue, and white; 750 ml capacity, 12.5 cm diameter, 4.5 cm height), 1 m apart from each other, filled with water and a drop of biodegradable dish soap with no fragrance. We did not perform standard transect observations since the sampling was performed by people with different skills, and due to

COVID-19 restrictions, it was not possible to work in teams. Pan traps were placed on the ground, in areas with short grass, so that they were clearly visible to pollinators. Pan traps were exposed for 48 h during sunny days, with low wind and temperatures > 20 °C. Wild pollinators were morphologically identified to the species or morphospecies level by DP (hoverflies), and AC and MM (wild bees). Wild pollinator samplings were repeated three times, once per month, between May and July 2021. Since pan traps are considered an unreliable method for estimating pollinator abundance (Portman et al., 2020; Westphal et al., 2008), we focused on pollinator diversity. We calculated α -diversity, *i.e.*, the number of wild pollinator species at each site, and γ -diversity, *i.e.*, the total number of wild pollinator species for each habitat type.

The cover and diversity of flowering plant species are strong indicators of habitat quality for pollinators, and can therefore be used as proxies for habitat enhancement for pollinators (von Königslöw et al., 2022; Wratten et al., 2012; Zamorano et al., 2020). At each site, we identified all flowering plant species in a 10-m radius buffer around the pan traps and assessed their relative abundance. The sampling was repeated three times, once per month, between May and July 2021. At each site, we then calculated flowering plant species α -diversity and mean flower cover.

2.3. Assessment of multiple ESs

Between April and September 2021, we measured eight indicators of seven ESs at each site. ESs were chosen based on the Common International Classification of Ecosystem Services (CICES) 5.1 categories and included provisioning, regulating and cultural ESs, mostly related to biodiversity (Table 1) (Haines-Young and Potschin, 2018). We chose a high number of ESs that are fundamental in both agricultural and natural areas (Garland et al., 2021), but are rarely assessed in urban environments (Pereira et al., 2023). Moreover, all selected ESs could be quickly and easily measured in all habitat types.

2.3.1. Honeybee-related ESs

The honeybee (*Apis mellifera* Linnaeus) is the most important managed pollinator species (Hung et al., 2018). ESs provided by honeybees include several regulating, provisioning, and cultural services. Since large-sized pollinators are often under-sampled using pan traps (Roulston et al., 2007), we opted for direct observations of honeybees on flowering plants to assess their abundance. At each site, we counted honeybees on flowers for 10 min. Honeybee samplings were repeated three times, once per month, between May and July 2021. At each site,

Table 1

List of the assessed ESs, with information on the corresponding Common International Classification of Ecosystem Services (CICES) 5.1 category and code (Haines-Young and Potschin, 2018) and the measured ES indicators.

ES	CICES 5.1 category	CICES 5.1 code	ES indicator (s)
1) Honeybee-related ESs	Provisioning, regulating, cultural	1.1.3.1, 2.2.2.1, 3.1.1.2, 3.1.1.3	Managed honeybee abundance
2) Ground-dwelling arthropod-related ESs	Regulating	2.2.2.2, 2.2.3.1	Ground-dwelling arthropod abundance
3) Pest control	Regulating	2.2.3.1	Dummy caterpillar predation rate
4) Seed predation	Regulating	2.2.2.2	Seed predation rate
5) Disease control	Regulating	2.2.3.2	Asian tiger mosquito egg abundance
6) Soil nutrient cycling	Regulating	2.2.4.2	Soil stabilisation factor S and decomposition rate k
7) Flood control	Regulating	2.2.1.3	Water infiltration rate in soil

we then calculated the total honeybee abundance.

2.3.2. Ground-dwelling arthropod-related ESs

Ground-dwelling arthropods include key groups of pest and seed predators (Bohan et al., 2011; Nyffeler and Birkhofer, 2017). We assessed ground-dwelling arthropod abundance using pitfall traps. At each site, we placed two pitfall traps, consisting of a buried plastic cup (500 ml capacity, 11 cm diameter, 15 cm height) protected by a plastic cover (Spence and Niemelä, 1994). Traps were activated with 70% ethylene glycol for four weeks from June to August 2021, for a total of three sampling rounds. Collected arthropods were stored in 75% ethanol and sorted in the laboratory. At each site, we then determined the total abundance of target ground-dwelling arthropods, *i.e.*, ground beetles (Coleoptera: Carabidae), rove beetles (Coleoptera: Staphylinidae), and spiders (Araneae).

2.3.3. Pest control

Pest control by natural enemies is a major regulating ES, especially in agroecosystems (Holland et al., 2016; Rega et al., 2018). Dummy caterpillars are commonly used to assess the intensity of pest predation by actively hunting sight predators (Howe et al., 2009). We moulded 30 mm × 3 mm dummy caterpillars using green plasticine and glued the caterpillars on wood skewers. We placed eight dummy caterpillars at each site, which were exposed for 72 h. The sampling was repeated two times, in June and July 2021. We then checked all predation marks on caterpillars and determined the mean predation rate of dummy caterpillars at each site.

2.3.4. Seed predation

We used seed cards to assess the intensity of predation of weed seeds by seed predators. Seed cards were made of small rectangles (8 × 3 cm) of P80 grit sandpaper, on which seeds were glued using a repositionable glue (3 M Spray Mount) (Westerman et al., 2003). On each seed card, we glued forty seeds of *Taraxacum officinale* (Weber) ex Wiggers, a native plant species, and forty seeds of *Oenothera biennis* L., an invasive exotic species. At each site, we placed three seed cards that were fixed to the ground using nails and were exposed for 72 h, during sunny days with low wind. Then, we collected the seed cards and counted the remaining seeds of each species. The sampling was repeated twice, in June and July 2021. At each site, we then estimated the mean seed predation rate.

A limitation of this study is that we assumed that weed seeds removed from the cards were predated, thus indicating a service, although we cannot ensure that the organisms that removed the seeds actually destroyed them. However, seed cards have been used for decades to specifically assess seed predation rather than dispersal (Brust and House, 1988; Westerman et al., 2003). Moreover, the most common predators of both *T. officinale* and *O. biennis* are insects (Anstett et al., 2014; Honek et al., 2005), such as ground beetles, which are key seed predators (Carbonne et al., 2020; Kulkarni et al., 2015). Seeds of both species are relatively small in size (weight of 1000 seeds for both species: 0.45 gr) and birds and rodents probably predated them to a minimal extent (Hulme, 1998).

2.3.5. Disease control

We used ovitraps to estimate the abundance of Asian tiger mosquitoes, *Aedes albopictus* (Skuse), a species of medical importance (Benedict et al., 2007). Ovitrap consisted of a small dark container (400 ml capacity, 8 cm diameter, 10 cm height) filled with water and containing a masonite stick where mosquitoes laid their eggs. At each site, we placed one ovitrap on the ground and exposed it for two weeks at the end of July 2021, during the peak season of egg laying (Petrić et al., 2021). Ovitrap were collected, and the number of eggs was counted using a stereoscope.

2.3.6. Soil nutrient cycling

We estimated the decomposition rate of organic matter in soil using

the Tea Bag Index (TBI) methodology (Keuskamp et al., 2013). We weighed the green tea and rooibos before placing the bags in the field. At the end of April 2021, we buried two pairs of bags in two 8-cm-deep holes at each site. For each pair, we used one green tea bag and one rooibos bag. After three months, at the end of July 2021, bags were collected, oven-dried at 65 °C for 48 h, and their contents were weighed. At each site, following the TBI protocol, we calculated the stabilisation factor *S* and the decomposition rate *k* (Keuskamp et al., 2013).

Since we were not able to collect all green tea and rooibos bags after three months, we had a few missing values for both the stabilisation factor and the decomposition rate, which we replaced with the respective averaged values to have the same number of measured ESs in all sites. However, to ensure that the use of averaged values would not affect the results of our models, we also performed all the statistical analyses excluding sites with missing bags, *i.e.*, those for which it was not possible to calculate soil stabilisation factor and/or soil decomposition rate. This sensitivity analysis indicated that all models did not show significant differences, therefore, we only present the results of models including averaged values.

2.3.7. Flood control

We assessed flood control by measuring the rate of water infiltration in soil (United States Department of Agriculture, 2014). The measurements were taken after the soil had been saturated by rain, in September 2021. At each site, we selected a spot with short grass, where we hammered a plastic tube (20 cm diameter) in the ground for about 10 cm. Then, we poured 1 L of water into the plastic tube and assessed the water depth at the beginning of the experiment and after 6 min to obtain the water infiltration rate. We repeated the process three times per site. At each site, we then calculated the mean water infiltration rate as the average value of the three trials.

2.4. Assessment of EMF

We assessed EMF at each site including measures for honeybee-related ESs, ground-dwelling arthropod-related ESs, pest control, seed predation, disease control, soil nutrient cycling, and flood control. We used two approaches: 1) the averaging approach (Mouillot et al., 2011), and 2) the multiple threshold approach (Byrnes et al., 2014). All statistical analyses were performed using R version 3.6.1 (R Core Team, 2019).

Using the averaging approach, we calculated a simple EMF index based on normalized values for each ES indicator. First, we normalized each ES indicator value by its maximum, using the formula $X_{norm} = (X_{raw} - X_{min}) / (X_{max} - X_{min})$, where X_{norm} is the normalized ES indicator value, X_{raw} is the raw ES indicator value, X_{min} is the minimum ES indicator value and X_{max} is the maximum ES indicator value. We considered as X_{min} and X_{max} the minimum and maximum ES indicator values observed over the whole dataset and including all three habitat types. For the abundance of Asian tiger mosquito eggs, the only indicator for which low values indicate higher levels of the ES, raw indicator values were reflected before normalization as $X_{ref} = X_{max} - X_{raw}$. Second, we calculated the averaged EMF index for each site as the mean value of all normalized indicator values. Averaged EMF was calculated using the R package *caret* (Kuhn, 2022).

The multiple threshold approach allows evaluating whether multiple functions are simultaneously performing at high levels. We considered the full range of thresholds, from 1% to 99% of the maximum value of each ES indicator, and then counted the number of ES indicators that surpassed each threshold at each site. To compute the multiple threshold EMF, we used the R package *multifunc* (Byrnes et al., 2014).

2.5. Statistical analyses

First, we visually assessed the differences among the three habitat types for wild pollinator α -diversity, flower cover, flowering plant

α -diversity and ES indicators. To do so, we compared normalized variable values among the three habitat types using a radar plot.

Second, we analysed how wild pollinator α -diversity and EMF changed in the three habitat types (indicator of habitat restoration) and in relation to flower cover (indicator of habitat enhancement). As flower cover and flowering plant α -diversity were strongly correlated (Pearson's correlation coefficient = 0.606, p -value < 0.001), we could not include both in the same models. Therefore, all models were run twice, first using flower cover as explanatory variable, and then using flowering plant α -diversity as explanatory variable. All models including flower cover showed a lower AIC, therefore, we chose flower cover as an indicator of habitat enhancement for pollinators. We built two linear mixed-effect models using wild pollinator α -diversity and averaged EMF as response variables, and habitat type and flower cover as explanatory variables. We also included the region ID as random factor. To run these models, we used the R package *nlme* (Pinheiro et al., 2019). Moreover, using the multiple threshold approach, we analysed the effect of habitat type and flower cover on the number of ESs beyond a certain level of performance. To visually assess the significance of each threshold, we calculated the slope of these relationships and plotted them against the corresponding threshold value. Figures were plotted using the R package *ggplot2* (Wickham, 2016).

Third, to quantify the relationships between wild pollinator α -diversity, flower cover, flowering plant α -diversity and ES indicators and test how these relationships changed among the three habitat types, we calculated the Pearson's correlation coefficients between pairs of variables within each habitat type. Correlations were plotted using the R package *corrplot* (Wei et al., 2017).

Landscape context, in particular the amount of semi-natural areas, could affect both wild pollinators and EMF. However, our study was not designed to explore the effect of landscape context, since due to COVID-19 restrictions during fieldwork, we could only sample sites relatively close to the area where the authors who did the fieldwork resided. Therefore, we decided to reduce as much as possible the variation in landscape composition during site selection. To evaluate any potential effect of landscape variables, we fitted three models for each response variable, i.e., wild pollinator α -diversity and averaged EMF, using maximized log-likelihood and compared them using Δ AICc. Model 1 included as explanatory variables habitat type and flower cover. Model 2 included as explanatory variable only the percentage of semi-natural habitats in a 250 m radius buffer around the sampling sites. Model 3 included as explanatory variables habitat type, flower cover, and the percentage of semi-natural habitats in a 250 m radius buffer around the sampling sites. For all response variables, the Δ AICc between Model 1 and Model 3 was below 2, indicating little improvement with the addition of landscape variables, while the difference between Model 1 and Model 2 was always above 2, indicating a better predictive power of local variables (Table S2).

3. Results

3.1. Wild pollinators

We collected 1516 wild pollinator individuals belonging to 144 species or morphospecies (Table S3). The most represented wild pollinator family was Halictidae, with 1080 individuals and 45 species collected, which included the three most abundant wild pollinator species, i.e., *Lasioglossum glabriusculum* (Morawitz) (295 individuals), *L. malachurum* (Kirby) (125 individuals), and *L. minutissimum* (Kirby) (118 individuals). While wild bees were relatively common, we only collected 96 hoverfly individuals belonging to 30 species.

3.2. Effect of habitat type on wild pollinators and EMF

Semi-natural patches were characterized by a higher provision of most ESs compared to crop field margins and urban green areas, and

results were similar for pollinators and flowering plants (Fig. 1, Table S4). However, the abundance of ground-dwelling arthropods was higher in crop field margins. Urban green areas generally showed the lowest variable values, except for honeybee abundance, flower cover and flowering plant α -diversity. Soil-related ESs were comparable among the three habitat types.

Habitat type affected both wild pollinator diversity and EMF. Wild pollinator α -diversity was comparable in semi-natural patches and crop field margins, and it was lower in urban green areas (Table 2a, Fig. 2a, S2a). However, wild pollinator γ -diversity was higher in semi-natural patches than in other habitats. We observed 111 wild pollinator species in semi-natural patches, 77 species in crop field margins, and only 59 species in urban green areas.

Averaged EMF was also higher in semi-natural patches and crop field margins (Table 2b, Fig. 2b, S2b). EMF calculated using the multiple threshold approach showed a similar response to habitat type. EMF in semi-natural patches and crop field margins was generally comparable at low thresholds, but their differences increased at higher thresholds, with semi-natural patches providing higher levels of multiple ESs (Table S5a, Fig. 3a, d). We observed no differences in multiple threshold EMF between crop field margins and urban green areas (Table S5b, Fig. 3b, e), while the comparison between semi-natural patches and urban green areas revealed higher values of EMF in semi-natural patches (Table S5c, Fig. 3c, f).

3.3. Effect of flower cover on wild pollinators and EMF

Wild pollinator α -diversity strongly increased with increasing flower cover (Table 2a, Fig. 4). On the other hand, flower cover did not affect averaged and multiple threshold EMF (Table 2b, S6, Fig. S3). To explain this result, we analysed the correlations between wild pollinator α -diversity, flower cover, flowering plant α -diversity, and ES indicators (Fig. S4). We highlighted several co-benefits (positive correlations) and only a few trade-offs (negative correlations) among variables in all habitat types. However, correlations changed depending on habitat type. In crop field margins, wild pollinator α -diversity showed a trade-off with infiltration rate, but we also observed synergies between honeybee abundance and flower cover, flower cover and soil decomposition indices, and abundance of ground arthropods and predation rate of dummy caterpillars (Fig. S4a). Semi-natural patches showed the lowest number of significant correlations among variables, of which only one was a trade-off, and we observed no significant relationships between wild pollinator α -diversity and other variables (Fig. S4b). In urban green areas, wild pollinator α -diversity was positively correlated to flowering plant α -diversity and ground-dwelling arthropod abundance, and

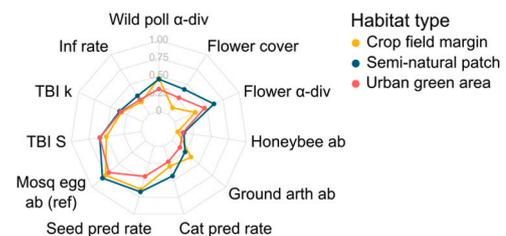


Fig. 1. Radar plot showing the mean normalized value of each variable at each habitat. Abbreviations are: “Wild poll α -div” for wild pollinator α -diversity, “Flower cover” for flowering plant cover, “Flower α -div” for flowering plant α -diversity, “Honeybee ab” for managed honeybee abundance (honeybee-related ESs), “Ground arth ab” for ground-dwelling arthropod abundance (ground-dwelling arthropod-related ESs), “Cat pred rate” for dummy caterpillar predation rate (pest control), “Seed pred rate” for seed predation rate (seed predation), “Mosq egg ab (ref)” for Asian tiger mosquito egg abundance (reflected) (disease control), “TBI S” for soil stabilisation factor S and “TBI k” for soil decomposition rate k (soil nutrient cycling), and “Inf rate” for water infiltration rate in soil (flood control).

Table 2

Results of the linear mixed-effect models assessing the effect of habitat type and flower cover on (a) wild pollinator α -diversity and (b) averaged EMF. The region ID was included as random factor in all models. Bold numbers indicate significant variables (p -value < 0.05).

	Estimate	SE	df	t-value	p-value
(a) Wild pollinator α-diversity					
Intercept (Crop field margin)	8.113	0.782	89	10.380	< 0.001
Semi-natural patch	-1.902	1.136	89	-1.674	0.098
Urban green area	-3.822	1.023	89	-3.735	< 0.001
Flower cover	0.128	0.047	89	2.751	0.007
(b) Averaged EMF					
Intercept (Crop field margin)	0.377	0.015	89	25.371	< 0.001
Semi-natural patch	0.037	0.022	89	1.626	0.108
Urban green area	-0.049	0.020	89	-2.434	0.017
Flower cover	0.001	0.001	89	1.558	0.123

negatively correlated to the abundance of Asian tiger mosquito eggs (Fig. S4c).

4. Discussion

To our knowledge, this is the first study investigating how conservation actions for pollinators, *i.e.*, habitat restoration and enhancement, affected EMF calculated using a considerable number of ESs. We found that habitat types supporting a higher diversity of wild pollinators were also associated with higher EMF. On the other hand, we did not find any relationship between flower cover and EMF in the three habitat types, meaning that improving local conditions for pollinators did not lead to higher EMF and indicating non-linear responses of multiple ESs.

4.1. Effect of habitat type on wild pollinators and EMF

Contrary to our expectations, we found that semi-natural patches and crop field margins hosted a comparable number of wild pollinator species. However, even if the number of species at each site was similar,

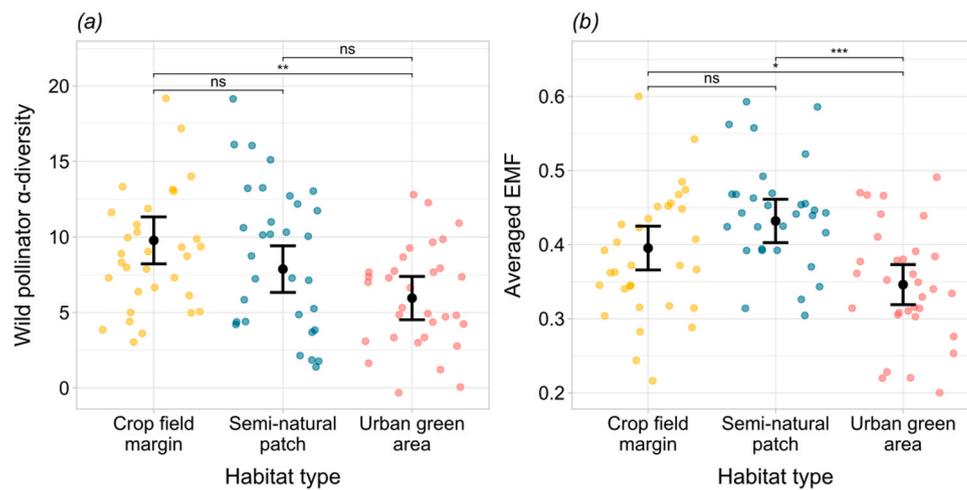


Fig. 2. Partial residual plots showing the effect of habitat type on (a) wild pollinator α -diversity and (b) averaged EMF. Coloured dots represent raw values, black dots represent expected values, and the error bars indicate 95% confidence intervals for the expected values of the variable.

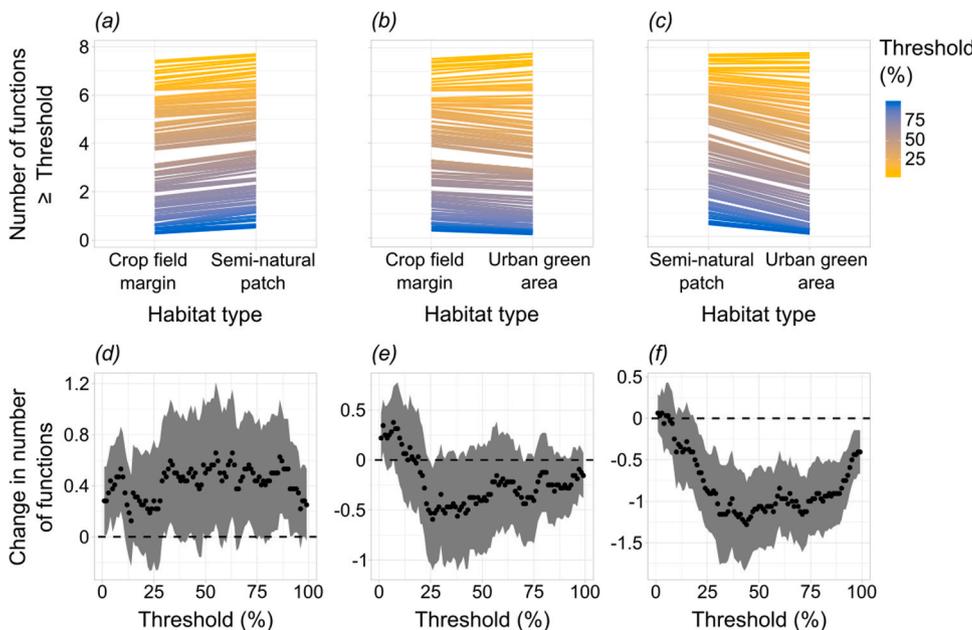


Fig. 3. Plots showing the effect of habitat type on multiple threshold EMF, *i.e.*, the number of ESs maximized at a certain threshold level. Panels (a) and (d) compare crop field margins and semi-natural patches, panels (b) and (e) compare crop field margins and urban green areas, and panels (c) and (f) compare semi-natural patches and urban green areas. Panels (a), (b), and (c) show the relationship between pairs of habitats and the number of functions that performed higher than a certain threshold. We considered the full range of thresholds, from 1% to 99% of the maximum value of each ES indicator, and each line represents a given threshold. Panels (d), (e), and (f) show the corresponding relationship between the threshold value and the slope of the relationship between habitat type and the number of functions reaching a certain threshold. Black dots represent fitted values, and the shading indicates 95% confidence intervals for the expected values of the variables. For each threshold, the relationship with habitat type is significant if the confidence interval does not overlap zero.

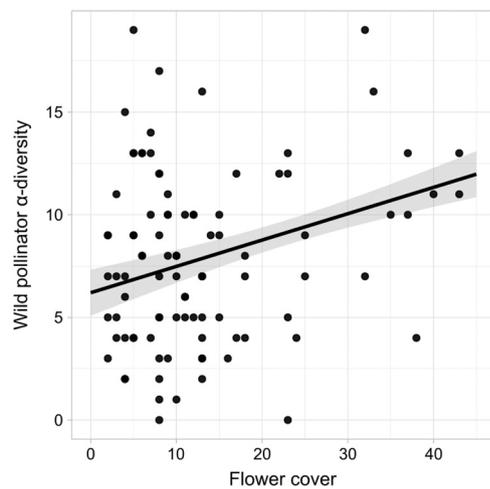


Fig. 4. Partial residual plot showing the effect of flower cover on wild pollinator α -diversity. Dots represent raw values, while the shading indicates 95% confidence intervals for the expected values of the variable.

the total species diversity of crop field margins was considerably lower, with 34 fewer pollinator species than in semi-natural patches, *i.e.*, species assemblages of field margins were more homogeneous and characterized by a low spatial turnover. Wild pollinators are usually negatively affected by agricultural intensification (Le Féon et al., 2010; Williams et al., 2010) since floral resources are often insufficient and the use of pesticides can pose a serious threat (Goulson et al., 2015). However, unmanaged field margins can be a crucial resource for pollinators in agricultural areas (Arnold et al., 2021; Slupik et al., 2022). In our study, we sampled both simple herbaceous field margins and complex field margins characterized by hedgerows and trees that might have boosted pollinator diversity (Aviron et al., 2023). Also, we found that urban green areas hosted the lowest number of pollinator species. This result is quite unexpected since recent studies highlighted the potential importance of urban areas for pollinators (Hall et al., 2017; Wenzel et al., 2020). However, these positive effects have been mostly reported for wild bees (but see Herrmann et al., 2023), while other pollinator groups such as hoverflies are known to be negatively affected by urbanization (Herrmann et al., 2023; Lagucki et al., 2017; Theodorou et al., 2020).

EMF also changed among the three habitat types. Averaged EMF showed comparable values in semi-natural patches and crop field margins and lower values in urban green areas. Semi-natural areas and, in general, habitats with a low management intensity have been shown to exhibit higher EMF (Lavorel et al., 2022; Moi et al., 2022; Olimpi et al., 2022). In particular, our crop field margins showed a high abundance of ground-dwelling arthropods and a high predation rate of seeds, as they often provide shelter and alternative prey (Allan et al., 2015; Samnegård et al., 2019). However, the multiple threshold approach revealed that at higher thresholds the difference between semi-natural patches and crop field margins was consistent, meaning that semi-natural patches, unlike crop field margins, were able to simultaneously provide high levels of multiple ESs. On the other hand, lower EMF values in urban green areas were expected, since regulating services have been shown to strongly decrease with increasing urbanization (Wang et al., 2019). Therefore, both wild pollinator diversity and EMF were maximized in semi-natural patches and crop field margins, also highlighting the potential role of field margins for sustaining pollinators while generating multiple environmental co-benefits (Mkenda et al., 2019). Habitat conversion from intensively managed to pollinator-friendly habitats might not be the only way to increase pollinator diversity and EMF.

4.2. Effect of flower cover on wild pollinators and EMF

As expected, we found a positive relationship between flower cover and wild pollinator α -diversity. Habitat enhancement for pollinators, *i.e.*, the increase in diversity and cover of flowering plant species, is an effective measure specifically designed to boost pollinator abundance and diversity in different habitat types (*e.g.*, Andrieu et al., 2018; Dietzel et al., 2023; Hussain et al., 2023; Morandin and Kremen, 2013; Woodcock et al., 2014; Zamorano et al., 2020) since floral resources are one of the central factors in shaping pollinator populations.

Contrary to our expectations, we did not find any relationship between flower cover and EMF. This is in contrast with other studies since habitat enhancement seems to benefit not only pollinators but also other ESs, especially those related to biodiversity (Wratten et al., 2012). Moreover, there is a large body of literature that showed positive relationships between biodiversity and EMF across different land use types, and most studies on the effect of above-ground biodiversity on EMF focused on plant species (Jing et al., 2015; Lefcheck et al., 2015; Maestre et al., 2012; Schittko et al., 2022; Soliveres et al., 2016; Zhou et al., 2022). However, here we did not sample the complete plant community, since we were only interested in understanding how flower cover and diversity, as indicators of habitat enhancement for pollinators, could affect EMF. Flower cover did not emerge as a good predictor of EMF, highlighting that improving the quality of existing habitats for pollinators does not positively affect EMF. Within the same habitat type, the analysis of the correlation among ESs indicated that probably the underlying drivers that promoted wild pollinator diversity were distinct from those promoting EMF. Moreover, the lack of consistent relationships among services within the three habitats suggested that specific drivers may lead to non-linear responses depending on the habitat type. For instance, pollinator-targeted interventions are often beneficial not only to pollinators but also predators of pests (Albrecht et al., 2020; Savage et al., 2021). However, sown flower strips do not always benefit pollinator populations as their effects may vary depending on the chosen flower mixture (Wood et al., 2015), and they might also increase the abundance of herbivores, resulting in a trade-off between pollination and pest control (Wäckers et al., 2007). Therefore, the net effects of pollinator-targeted interventions are not straightforward, and it is crucial to investigate which drivers determine high levels of different ESs among habitats (Bullock et al., 2021).

5. Conclusions

Maximising the delivery of multiple ESs across different habitat types is a complex task, but it is of central importance for the well-being of humans and ecosystems across human-impacted landscapes. Here, we showed that both semi-natural patches and crop field margins were associated with higher pollinator diversity and EMF, highlighting not only the key role of undisturbed habitats but also the potential importance of field margins. Nevertheless, it is fundamental to emphasise that the total diversity of pollinator species collected in crop field margins was much lower than in semi-natural patches, which are therefore able to support more heterogeneous pollinator communities. Moreover, we found no association between flower cover and EMF in any of the three investigated habitats, meaning that improving habitat quality for pollinators revealed to be insufficient to enhance EMF. Our study indicated that promoting pollinators does not always increase the number of co-benefits that could be delivered to society. Future investigations are needed to understand how pollinator interventions could affect ESs and EMF in different habitat types, and how landscape composition and structure could modulate these relationships.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108615](https://doi.org/10.1016/j.agee.2023.108615).

References

- Aguilar, R., Ashworth, L., Galetto, L., Aizen, M.A., 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* 9, 968–980. <https://doi.org/10.1111/j.1461-0248.2006.00927.x>.
- Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D.A., Loeb, G.M., Marini, L., Mc Kerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlöf, M., Sardiñas, H., Scilligo, A., Thies, C., Tschamntke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., Sutter, L., 2020. The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. *Ecol. Lett.* 23, 1488–1498. <https://doi.org/10.1111/ele.13576>.
- Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N., Böhm, S., Grassein, F., Hölzel, N., Klaus, V.H., Kleinebecker, T., Morris, E.K., Oelmann, Y., Prati, D., Renner, S.C., Rillig, M.C., Schaefer, M., Schloter, M., Schmitt, B., Schöning, I., Schrupf, M., Solly, E., Sorkau, E., Steckel, J., Steffen-Dewenter, I., Stempfhuber, B., Tschapka, M., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Fischer, M., 2015. Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecol. Lett.* 18, 834–843. <https://doi.org/10.1111/ele.12469>.
- Andrieu, E., Cabanettes, A., Alignier, A., Van Halder, I., Alard, D., Archaux, F., Barbaro, L., Bouget, C., Bailey, S., Corcket, E., Deconchat, M., Vigan, M., Villemey, A., Ouin, A., 2018. Edge contrast does not modulate edge effect on plants and pollinators. *Basic Appl. Ecol.* 27, 83–95. <https://doi.org/10.1016/j.baee.2017.11.003>.
- Anstett, D.N., Naujokaitis-Lewis, I., Johnson, M.T.J., 2014. Latitudinal gradients in herbivory on *Oenothera biennis* vary according to herbivore guild and specialization. *Ecology* 95, 2915–2923. <https://doi.org/10.1890/13-0932.1>.
- Arnold, S.E.J., Elisante, F., Mkenda, P.A., Tembo, Y.L.B., Ndakidemi, P.A., Gurr, G.M., Darbyshire, I.A., Belmain, S.R., Stevenson, P.C., 2021. Beneficial insects are associated with botanically rich margins with trees on small farms. *Sci. Rep.* 11, 15190. <https://doi.org/10.1038/s41598-021-94536-3>.
- Aviron, S., Berry, T., Leroy, D., Savary, G., Alignier, A., 2023. Wild plants in hedgerows and weeds in crop fields are important floral resources for wild flower-visiting insects, independently of the presence of intercrops. *Agric. Ecosyst. Environ.* 348, 108410. <https://doi.org/10.1016/j.agee.2023.108410>.
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L. M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects, 20142849 *Proc. R. Soc. B Biol. Sci.* 282. <https://doi.org/10.1098/rspb.2014.2849>.
- Baral, H., Keenan, R.J., Sharma, S.K., Stork, N.E., Kasel, S., 2014. Spatial assessment and mapping of biodiversity and conservation priorities in a heavily modified and fragmented production landscape in north-central Victoria, Australia. *Ecol. Indic.* 36, 552–562. <https://doi.org/10.1016/j.ecoind.2013.09.022>.
- Bauer, D.M., Sue Wing, I., 2016. The macroeconomic cost of catastrophic pollinator declines. *Ecol. Econ.* 126, 1–13. <https://doi.org/10.1016/j.ecolecon.2016.01.011>.
- Benedict, M.Q., Levine, R.S., Hawley, W.A., Lounibos, L.P., 2007. Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*. *Vector-Borne Zoonotic Dis.* 7, 76–85. <https://doi.org/10.1089/vbz.2006.0562>.
- Bohan, D.A., Boursault, A., Brooks, D.R., Petit, S., 2011. National-scale regulation of the weed seedbank by carabid predators. *J. Appl. Ecol.* 48, 888–898. <https://doi.org/10.1111/j.1365-2664.2011.02008.x>.
- Brittain, C., Williams, N., Kremen, C., Klein, A.M., 2013. Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proc. R. Soc. B Biol. Sci.* 280, 1–7. <https://doi.org/10.1098/rspb.2012.2767>.
- Brust, G.E., House, G.J., 1988. Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. *Am. J. Altern. Agric.* 3, 19–25. <https://doi.org/10.1017/S0889189300002083>.
- Bullock, J.M., McCracken, M.E., Bowes, M.J., Chapman, R.E., Graves, A.R., Hinsley, S.A., Hutchins, M.G., Nowakowski, M., Nicholls, D.J.E., Oakley, S., Old, G.H., Ostle, N.J., Redhead, J.W., Woodcock, B.A., Bedwell, T., Mayes, S., Robinson, V.S., Pywell, R.F., 2021. Does agri-environmental management enhance biodiversity and multiple ecosystem services?: a farm-scale experiment. *Agric. Ecosyst. Environ.* 320, 107582. <https://doi.org/10.1016/j.agee.2021.107582>.
- Byrnes, J.E.K., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., Cardinale, B.J., Hooper, D.U., Dee, L.E., Emmett Duffy, J., 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. *Methods Ecol. Evol.* 5, 111–124. <https://doi.org/10.1111/2041-210X.12143>.
- Carbonne, B., Petit, S., Neidel, V., Foffova, H., Daouti, E., Frei, B., Skuhrovec, J., Rezáč, M., Saska, P., Wallinger, C., Traugott, M., Bohan, D.A., 2020. The resilience of weed seedbank regulation by carabid beetles, at continental scales, to alternative prey. *Sci. Rep.* 10, 19315. <https://doi.org/10.1038/s41598-020-76305-w>.
- Fan, K., Chu, H., Eldridge, D.J., Gaitan, J.J., Liu, Y.R., Sokoya, B., Wang, J.T., Hu, H.W., He, J.Z., Sun, W., Cui, H., Alfaro, F.D., Abades, S., Bastida, F., Díaz-López, M., Bamigboye, A.R., Berdugo, M., Blanco-Pastor, J.L., Grebenc, T., Duran, J., Illán, J.G., Makhalyane, T.P., Mukherjee, A., Nahberger, T.U., Peñaloza-Bojacá, G.F., Plaza, C., Verma, J.P., Rey, A., Rodríguez, A., Siebe, C., Teixido, A.L., Trivedi, P., Wang, L., Wang, J., Yang, T., Zhou, X.Q., Zhou, X., Zaady, E., Tedersoo, L., Delgado-Baquerizo, M., 2023. Soil biodiversity supports the delivery of multiple ecosystem functions in urban greenspaces. *Nat. Ecol. Evol.* 7, 113–126. <https://doi.org/10.1038/s41559-022-01935-4>.
- Galler, C., von Haaren, C., Albert, C., 2015. Optimizing environmental measures for landscape multifunctionality: effectiveness, efficiency and recommendations for agri-environmental programs. *J. Environ. Manag.* 151, 243–257. <https://doi.org/10.1016/j.jenvman.2014.12.011>.
- Gamfeldt, L., Roger, F., 2017. Revisiting the biodiversity-ecosystem multifunctionality relationship. *Nat. Ecol. Evol.* 1, 1–7. <https://doi.org/10.1038/s41559-017-0168>.
- Garibaldi, L.A., Steffan-dewenter, L., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G.L.G., 2014. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608–1611. <https://doi.org/10.1126/science.1230200>.
- Garland, G., Banerjee, S., Edlinger, A., Miranda Oliveira, E., Herzog, C., Wittwer, R., Philippot, L., Maestre, F.T., van der Heijden, M.G.A., Heijden, M.G.A., 2021. A closer look at the functions behind ecosystem multifunctionality: a review. *J. Ecol.* 109, 600–613. <https://doi.org/10.1111/1365-2745.13511>.
- Gill, R.J., Baldock, K.C.R., Brown, M.J.F., Cresswell, J.E., Dicks, L.V., Fountain, M.T., Garratt, M.P.D., Gough, L.A., Heard, M.S., Holland, J.M., Ollerton, J., Stone, G.N., Tang, C.Q., Vanbergen, A.J., Vogler, A.P., Woodward, G., Arce, A.N., Boatman, N.D., Brand-Hardy, R., Breeze, T.D., Green, M., Hartfield, C.M., O'Connor, R.S., Osborne, J.L., Phillips, J., Sutton, P.B., Potts, S.G., 2016. Protecting an ecosystem service: approaches to understanding and mitigating threats to wild insect pollinators. In: *Advances in Ecological Research*. Elsevier Ltd, pp. 135–206. <https://doi.org/10.1016/bs.aecr.2015.10.007>.
- Gomes, L.C., Bianchi, F.J.J.A., Cardoso, I.M., Fernandes Filho, E.I., Schulte, R.P.O., 2020. Land use change drives the spatio-temporal variation of ecosystem services and their interactions along an altitudinal gradient in Brazil. *Landscape Ecol.* 35, 1571–1586. <https://doi.org/10.1007/s10980-020-01037-1>.
- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347, 1435–1444. <https://doi.org/10.1126/science.1255957>.
- Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahn, K., Arduser, M., Ascher, J.S., Baldock, K.C.R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.L., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G.N., Threlfall, C.G., 2017. The city as a refuge for insect pollinators. *Conserv. Biol.* 31, 24–29. <https://doi.org/10.1111/cobi.12840>.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., De Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12, e0185809. <https://doi.org/10.1371/journal.pone.0185809>.
- Herrmann, J., Buchholz, S., Theodorou, P., 2023. The degree of urbanisation reduces wild bee and butterfly diversity and alters the patterns of flower-visitation in urban dry grasslands. *Sci. Rep.* 13, 2702. <https://doi.org/10.1038/s41598-023-29275-8>.
- Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.-C.C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. *Pest Manag. Sci.* 72, 1638–1651. <https://doi.org/10.1002/ps.4318>.
- Honek, A., Martinkova, Z., Saska, P., 2005. Post-dispersal predation of *Taraxacum officinale* (dandelion) seed. *J. Ecol.* 93, 345–352. <https://doi.org/10.1111/j.1365-2745.2005.00987.x>.
- Howe, A., Lövei, G.L., Nachman, G., 2009. Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomol. Exp. Appl.* 131, 325–329. <https://doi.org/10.1111/j.1570-7458.2009.00860.x>.
- Hulme, P.E., 1998. Post-dispersal seed predation and seed bank persistence. *Seed Sci. Res.* 8, 513–519. <https://doi.org/10.1017/S0960258500004487>.
- Hung, K.-L.J., Kingston, J.M., Albrecht, M., Holway, D.A., Kohn, J.R., 2018. The worldwide importance of honey bees as pollinators in natural habitats. *Proc. R. Soc. B Biol. Sci.* 285, 20172140. <https://doi.org/10.1098/rspb.2017.2140>.
- Hussain, R.I., Walcher, R., Vogel, N., Krautler, B., Rasran, L., Frank, T., 2023. Effectiveness of flowers strips on insect's restoration in intensive grassland. *Agric. Ecosyst. Environ.* 348, 108436. <https://doi.org/10.1016/j.agee.2023.108436>.
- Jing, X., Sanders, N.J., Shi, Y., Chu, H., Classen, A.T., Zhao, K., Chen, L., Shi, Yue, Jiang, Y., He, J.-S., 2015. The links between ecosystem multifunctionality and

- above- and belowground biodiversity are mediated by climate. *Nat. Commun.* 6, 8159. <https://doi.org/10.1038/ncomms9159>.
- Keuskamp, J.A., Dingemans, B.J.J., Lehtinen, T., Sarneel, J.M., Hefting, M.M., 2013. Tea bag index: a novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol. Evol.* 4, 1070–1075. <https://doi.org/10.1111/2041-210X.12097>.
- Klaus, F., Tschardtke, T., Bischoff, G., Grass, I., 2021. Floral resource diversification promotes solitary bee reproduction and may offset insecticide effects – evidence from a semi-field experiment. *Ecol. Lett.* 24, 668–675. <https://doi.org/10.1111/ele.13683>.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschardtke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kuhn, M., 2022. *Caret: classification and regression training*. R. Package Version 6, 0–93.
- Kulkarni, S.S., Dossdall, L.M., Willenborg, C.J., 2015. The role of ground beetles (Coleoptera: Carabidae) in weed seed consumption: a review. *Weed Sci.* 63, 355–376. <https://doi.org/10.1614/WS-D-14-00067.1>.
- Lagucki, E., Burdine, J.D., McCluney, K.E., 2017. Urbanization alters communities of flying arthropods in parks and gardens of a medium-sized city. *PeerJ* 5, e3620. <https://doi.org/10.7717/peerj.3620>.
- Laura, V.V., Bert, R., Steven, B., Pieter, D.F., Victoria, N., Paul, P., Kris, V., 2017. Ecosystem service delivery of agri-environment measures: a synthesis for hedgerows and grass strips on arable land. *Agric. Ecosyst. Environ.* 244, 32–51. <https://doi.org/10.1016/j.agee.2017.04.015>.
- Lavorel, S., Grigulis, K., Richards, D.R., Etherington, T.R., Law, R.M., Herzog, A., 2022. Templates for multifunctional landscape design. *Landsc. Ecol.* 37, 913–934. <https://doi.org/10.1007/s10980-021-01377-6>.
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agric. Ecosyst. Environ.* 137, 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>.
- Lefcheck, J.S., Byrnes, J.E.K.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Hensel, M.J.S.S., Hector, A., Cardinale, B.J., Duffy, J.E., 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. *Nat. Commun.* 6, 6936. <https://doi.org/10.1038/ncomms7936>.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and human well-being: synthesis*. Island Press, Washington, DC.
- R. Core Team, 2019. *R: A language and environment for statistical computing*.
- Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F., Berhe, A.A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., He, J.-Z., Hseu, Z.-Y., Hu, H.-W., Kirchmair, M., Neuhauser, S., Pérez, C.A., Reed, S.C., Santos, F., Sullivan, B.W., Trivedi, P., Wang, J.-T., Weber-Grullon, L., Williams, M.A., Singh, B.K., 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. *Nat. Ecol. Evol.* 4, 210–220. <https://doi.org/10.1038/s41559-019-1084-y>.
- Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023. Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. *Ecol. Indic.* 147, 109980. <https://doi.org/10.1016/j.ecolind.2023.109980>.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1, 1–10. <https://doi.org/10.1126/sciadv.1500052>.
- Haines-Young, R., Potschin, M.B., 2018. *Common International Classification of Ecosystem Services (CICES) V5. 1 and guidance on the application of the revised structure*.
- Lemanski, N.J., Williams, N.M., Winfree, R., 2022. Greater bee diversity is needed to maintain crop pollination over time. *Nat. Ecol. Evol.* 6, 1516–1523. <https://doi.org/10.1038/s41559-022-01847-3>.
- Maes, J., Paracchini, M.L., Zulian, G., Dunbar, M.B., Alkemade, R., 2012. Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. *Biol. Conserv.* 155, 1–12. <https://doi.org/10.1016/j.biocon.2012.06.016>.
- Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gabriel Gatica, M., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Moneris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335, 214–218. <https://doi.org/10.1126/science.1215442>.
- Mensah, S., Salako, K.V., Assogbadjo, A., Glèlè Kakaï, R., Sinsin, B., Seifert, T., 2020. Functional trait diversity is a stronger predictor of multifunctionality than dominance: Evidence from an Afrotropical forest in South Africa. *Ecol. Indic.* 115, 106415. <https://doi.org/10.1016/j.ecolind.2020.106415>.
- Mkenda, P.A., Ndakidemi, P.A., Mbega, E., Stevenson, P.C., Arnold, S.E.J., Gurr, G.M., Belmain, S.R., 2019. Multiple ecosystem services from field margin vegetation for ecological sustainability in agriculture: scientific evidence and knowledge gaps. *PeerJ* 7, e8091. <https://doi.org/10.7717/peerj.8091>.
- Moi, D.A., Lansac-Tôha, F.M., Romero, G.Q., Sobral-Souza, T., Cardinale, B.J., Kratina, P., Perkins, D.M., Teixeira de Mello, F., Jeppesen, E., Heino, J., Lansac-Tôha, F.A., Velho, L.F.M., Mormul, R.P., 2022. Human pressure drives biodiversity–multifunctionality relationships in large Neotropical wetlands. *Nat. Ecol. Evol.* 6, 1279–1289. <https://doi.org/10.1038/s41559-022-01827-7>.
- Morandini, L.A., Kremen, C., 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl.* 23, 829–839. <https://doi.org/10.1890/12-1051.1>.
- Mouillot, D., Villéger, S., Scherer-Lorenzen, M., Mason, N.W.H., 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS One* 6, e17476. <https://doi.org/10.1371/journal.pone.0017476>.
- Nyffeler, M., Birkhofer, K., 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *Sci. Nat.* 104, 30. <https://doi.org/10.1007/s00114-017-1440-1>.
- Olimpi, E.M., Garcia, K., Gonthier, D.J., Kremen, C., Snyder, W.E., Wilson-Rankin, E.E., Karp, D.S., 2022. Semi-natural habitat surrounding farms promotes multifunctionality in avian ecosystem services. *J. Appl. Ecol.* 59, 898–908. <https://doi.org/10.1111/1365-2664.14124>.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals. *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Pereira, P., Yin, C., Hua, T., 2023. Nature-based solutions, ecosystem services, disservices, and impacts on well-being in urban environments. *Curr. Opin. Environ. Sci. Heal* 33, 100465. <https://doi.org/10.1016/j.coesh.2023.100465>.
- Petrić, M., Ducheyne, E., Gossner, C.M., Marsboom, C., Nicolas, G., Venail, R., Hendrickx, G., Schaffner, F., 2021. Seasonality and timing of peak abundance of *Aedes albopictus*. *Eur. J. Implic. Public Anim. Health Geospat. Health* 16. <https://doi.org/10.4081/gh.2021.996>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Core Team, R., 2019. *nlme: linear and nonlinear mixed effects models*. R. Package Version 3, 1–140. (<https://CRAN.R-project.org/package=nlme>).
- Portman, Z.M., Bruninga-Socolar, B., Cariveau, D.P., 2020. The state of bee monitoring in the United States: a call to refocus away from bowl traps and towards more effective methods. *Ann. Entomol. Soc. Am.* 113, 337–342. <https://doi.org/10.1093/aesa/saaa010>.
- Rega, C., Bartual, A.M., Bocci, G., Sutter, L., Albrecht, M., Moonen, A.C., Jeanneret, P., van der Werf, W., Pfister, S.C., Holland, J.M., Paracchini, M.L., 2018. A pan-European model of landscape potential to support natural pest control services. *Ecol. Indic.* 90, 653–664. <https://doi.org/10.1016/j.ecolind.2018.03.075>.
- Reilly, J.R., Artz, D.R., Biddinger, D., Bobiwash, K., Boyle, N.K., Brittain, C., Brokaw, J., Campbell, J.W., Daniels, J., Elle, E., Ellis, J.D., Fleischer, S.J., Gibbs, J., Gillespie, R. L., Gundersen, K.B., Gut, L., Hoffman, G., Joshi, N., Lundin, O., Mason, K., McGrady, C.M., Peterson, S.S., Pitts-Singer, T.L., Rao, S., Rothwell, N., Rowe, L., Ward, K.L., Williams, N.M., Wilson, J.K., Isaacs, R., Winfree, R., 2020. Crop production in the USA is frequently limited by a lack of pollinators. *Proc. R. Soc. B Biol. Sci.* 287, 2–9. <https://doi.org/10.1098/rspb.2020.0922>.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, A.M., Kremen, C., Bogdanskii, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandini, L.A., Ochieng', A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns. *Ecol. Lett.* 11, 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>.
- Roulston, T.H., Smith, S.A., Brewster, A.L., 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee fauna. *J. Kans. Entomol. Soc.* 80, 179–181. <https://www.jstor.org/stable/25086376>.
- Rusch, A., Binet, D., Delbac, L., Thiéry, D., 2016. Local and landscape effects of agricultural intensification on carabid community structure and weed seed predation in a perennial cropping system. *Landsc. Ecol.* 31, 2163–2174. <https://doi.org/10.1007/s10980-016-0390-x>.
- Samnegård, U., Alins, G., Boreux, V., Bosch, J., García, D., Happe, A., Klein, A., Miñarro, M., Mody, K., Porcel, M., Rodrigo, A., Roquer-Beni, L., Tassin, M., Hambäck, P.A., 2019. Management trade-offs on ecosystem services in apple orchards across Europe: direct and indirect effects of organic production. *J. Appl. Ecol.* 56, 802–811. <https://doi.org/10.1111/1365-2664.13292>.
- Savage, J., Woodcock, B.A., Bullock, J.M., Nowakowski, M., Talloun, J.R.B., Pywell, R. F., 2021. Management to support multiple ecosystem services from productive grasslands. *Sustainability* 13, 6263. <https://doi.org/10.3390/su13116263>.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. *Ecol. Lett.* 16, 912–920. <https://doi.org/10.1111/ele.12128>.
- Schittko, C., Onandia, G., Bernard-Verdier, M., Heger, T., Jeschke, J.M., Kowarik, I., Maaß, S., Joshi, J., 2022. Biodiversity maintains soil multifunctionality and soil organic carbon in novel urban ecosystems. *J. Ecol.* 110, 916–934. <https://doi.org/10.1111/1365-2745.13852>.
- Slupik, O., McCune, F., Watson, C., Proulx, R., Fournier, V., 2022. Response of bee and hoverfly populations to a land-use gradient in a Quebec floodplain. *J. Insect Conserv.* 26, 919–932. <https://doi.org/10.1007/s10841-022-00437-9>.
- Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Hölzel, N., Jung, K., Klaus, V.H., Kleinebecker, T., Klemmer, S., Krauss, J., Lange, M., Morris, E. K., Müller, J., Oelmann, Y., Overmann, J., Pašalić, E., Rillig, M.C., Schaefer, H.M., Schloter, M., Schmitt, B., Schöning, I., Schruppf, M., Sikorski, J., Socher, S.A., Solly, E.F., Sonnemann, I., Sorkau, E., Steckel, J., Steffan-Dewenter, I., Stempfhuber, B., Tschapka, M., Türke, M., Venter, P.C., Weiner, C.N., Weisser, W.W., Werner, M., Westphal, C., Wilcke, W., Wolters, V., Wubet, T., Wurst, S., Fischer, M.,

- Allan, E., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* 536, 456–459. <https://doi.org/10.1038/nature19092>.
- Spence, J.R., Niemelä, J.K., 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. Entomol.* 126, 881–894. <https://doi.org/10.4039/Ent126881-3>.
- Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G., Albrecht, M., 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *J. Appl. Ecol.* 54, 1856–1864. <https://doi.org/10.1111/1365-2664.12907>.
- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T.E., Paxton, R.J., 2020. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat. Commun.* 11, 1–13. <https://doi.org/10.1038/s41467-020-14496-6>.
- Tonietto, R.K., Larkin, D.J., 2018. Habitat restoration benefits wild bees: a meta-analysis. *J. Appl. Ecol.* 55, 582–590. <https://doi.org/10.1111/1365-2664.13012>.
- Tóth, Z., Hornung, E., Baldi, A., 2018. Effects of set-aside management on certain elements of soil biota and early stage organic matter decomposition in a High Nature Value Area, Hungary. *Nat. Conserv.* 29, 1–26. <https://doi.org/10.3897/natureconservation.29.24856>.
- United States Department of Agriculture, 2014. Soil infiltration: Soil health.
- von Königslöw, V., Fornoff, F., Klein, A.-M., 2022. Pollinator enhancement in agriculture: comparing sown flower strips, hedges and sown hedge herb layers in apple orchards. *Biodivers. Conserv.* 31, 433–451. <https://doi.org/10.1007/s10531-021-02338-w>.
- Wäckers, F.L., Romeis, J., Van Rijn, P., 2007. Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. *Annu. Rev. Entomol.* 52, 301–323. <https://doi.org/10.1146/annurev.ento.52.110405.091352>.
- Wang, J., Zhou, W., Pickett, S.T.A., Yu, W., Li, W., 2019. A multiscale analysis of urbanization effects on ecosystem services supply in an urban megaregion. *Sci. Total Environ.* 662, 824–833. <https://doi.org/10.1016/j.scitotenv.2019.01.260>.
- Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., Zemla, J., 2017. R package “corrplot”: visualization of a correlation matrix. *Statistician* 56, 316–324.
- Wenzel, A., Grass, I., Belavadi, V.V., Tschamtker, T., 2020. How urbanization is driving pollinator diversity and pollination – a systematic review. *Biol. Conserv.* 241, 108321 <https://doi.org/10.1016/j.biocon.2019.108321>.
- Westerman, P.R., Wes, J.S., Kropff, M.J., Van Der Werf, W., 2003. Annual losses of weed seeds due to predation in organic cereal fields. *J. Appl. Ecol.* 40, 824–836. <https://doi.org/10.1046/j.1365-2664.2003.00850.x>.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, L., 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.* 78, 653–671. <https://doi.org/10.1890/07-1292.1>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York, NY, New York.
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143, 2280–2291. <https://doi.org/10.1016/j.biocon.2010.03.024>.
- Wood, T.J., Holland, J.M., Goulson, D., 2015. Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biol. Conserv.* 187, 120–126. <https://doi.org/10.1016/j.biocon.2015.04.022>.
- Woodcock, B.A., Savage, J., Bullock, J.M., Nowakowski, M., Orr, R., Tallwin, J.R.B., Pywell, R.F., 2014. Enhancing floral resources for pollinators in productive agricultural grasslands. *Biol. Conserv.* 171, 44–51. <https://doi.org/10.1016/j.biocon.2014.01.023>.
- Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E., Desneux, N., 2012. Pollinator habitat enhancement: benefits to other ecosystem services. *Agric. Ecosyst. Environ.* 159, 112–122. <https://doi.org/10.1016/j.agee.2012.06.020>.
- Zamorano, J., Bartomeus, I., Grez, A.A., Garibaldi, L.A., 2020. Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conserv. Divers.* 13, 519–531. <https://doi.org/10.1111/icad.12454>.
- Zhou, G., Lucas-Borja, M.E., Liu, S., Hu, H., He, J., Wang, X., Jiang, Z., Zhou, X., Delgado-Baquerizo, M., 2022. Plant and soil biodiversity are essential for supporting highly multifunctional forests during Mediterranean rewilding. *Funct. Ecol.* 37, 420–431. <https://doi.org/10.1111/1365-2435.14230>.