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Butterflies as indicators of restoration success: insights from habitat restoration in agricultural landscapes

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Abstract

Introduction: Conservation strategies to support pollination service in agricultural landscapes increasingly rely on habitat restoration to mitigate biodiversity loss and support pollinator populations. However, the effectiveness of such measures depends on pollinator traits and landscape context.

Objectives: This study evaluated the impact of habitat restoration on butterfly (Lepidoptera: Papilionoidea and Hesperioidea) and bumblebee communities (Hymenoptera: Apidae: *Bombus* spp.), recognized as key pollinator indicators. The research was conducted on nine farms in northern Italy, where restoration efforts focused on establishing pollinator-friendly habitats, including species-rich grasslands and flower strips.

Methods: Monitoring was conducted along transects subdivided into restored and unrestored sub-transects. High-resolution land cover data were used to assess landscape composition at both local and landscape scales. Surveys were conducted monthly from May to September, before (2022) and after (2023) restoration. Linear mixed models were used to analyze the effects of the percent cover of restored habitat area and landscape composition on pollinator species richness and abundance.

Results: Restoration positively affected pollinator communities, although responses varied between the two pollinator groups. Butterflies showed clear increases in richness and abundance in relation to percent cover of both restored habitat area and land cover/land use types, while bumblebee responses were less marked. A beneficial effect of restoration measures on unrestored areas was observed for butterflies, with higher richness and abundance also in adjacent unrestored areas.

Conclusions: The contrasting responses observed between butterflies and bumblebees emphasize the value of butterflies as sensitive bioindicators of habitat restoration success.

Implications for Practice: Habitat restoration can produce detectable benefits for pollinator communities within a single year from intervention. The effectiveness of rapid assessments depends strongly on the choice of indicator group. Butterflies provide a reliable, cost-effective means of evaluating restoration outcomes, capturing both local and landscape-scale responses not observed for bumblebees over the same period. This finding is particularly relevant given the growing demand for standardized monitoring outputs within short reporting cycles in restoration and agri-environment programs. Including butterflies in standardized monitoring frameworks, as envisaged under the European Union (EU) Nature Restoration Law and the EU Pollinators Initiative, can improve biodiversity tracking and support evidence-based restoration planning in agricultural landscapes.

Key words: bumblebees, ecological intensification, habitat restoration, landscape heterogeneity, life-history traits, pollinators

Introduction

In recent decades, there has been a growing global emphasis on the need to shift agricultural practices toward ecological intensification in order to reduce the negative impacts of agriculture on the environment, conserve biodiversity in agroecosystems (Batáry et al. 2015; MacLaren et al. 2022), and improve associated ecosystem services while maintaining or even increasing yields (Kleijn et al. 2019).

Among ecosystem services, pollination is crucial for the long-term survival of wild plant populations (Ollerton et al. 2011) and crop production (Garibaldi et al. 2014). In the agricultural landscape, the erosion of plant species richness and the concomitant reduction in both the quantity and quality of suitable natural and seminatural habitats has been identified as a major driver of pollinator population decline (Ockermüller et al. 2023). In response, conservation strategies aimed at supporting wild pollinator communities increasingly emphasize landscape-scale restoration, including the reestablishment and proper management of high quality seminatural habitats such as wildflower strips and species-rich grasslands (Morandin & Kremen 2013; Tonietto & Larkin 2018; Hussain et al. 2022), which are key habitats for providing diversified trophic resources and nesting sites essential for a wide range of pollinator species (Villemey et al. 2015; Söderman et al. 2018).

Author contributions: SF conceived the research and performed data collection; SF, EF, GB designed the research; SF, ADB analyzed the data; SF, EF, GB wrote the manuscript.

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Overall, habitat restoration has been shown to increase species richness and abundance of key pollinator groups. A global meta-analysis of habitat restoration projects (Tonietto & Larkin 2018) demonstrated consistent positive effects on wild bee abundance and richness across multiple habitat types. Likewise, a synthesis of 25 large-scale studies found that grassland restoration significantly increased pollinator abundance and richness, often reaching values comparable to those observed in remnant sites, with lepidopterans showing particularly strong responses (Sexton & Emery 2020). However, significant challenges and knowledge gaps remain regarding the optimal design of restoration interventions (Kleijn et al. 2019; Faichnie et al. 2021), as their effectiveness in enhancing pollinator communities may depend on a range of factors operating at different levels of organization and scale (Faichnie et al. 2021; Woodcock et al. 2021).

Arguably, pollinator life-history traits such as resource requirements, mobility and specialization in nesting and overwintering habitats can lead to different outcomes of restoration measures for pollinator communities (Kremen & M'Gonigle 2015; Öckinger et al. 2018). Pollinators that exhibit generalist foraging behavior, that is, that are able to exploit the floral resources of a wide range of plant species and exhibit high mobility, are expected to colonize newly established or improved seminatural habitats more effectively than specialist species due to their broader ecological niches (Aviron et al. 2011). Apart from foraging strategies, pollinator species exhibit significant differences in their nesting and overwintering requirements, which are critical to their ability to establish and maintain viable populations in restored habitats. For instance, butterflies and flies do not build nests but require host plants and habitat features that support the development of their larval stages, often with high specificity (Altermatt & Pearse 2011; Moquet et al. 2018). In contrast, wild bees and bumblebees require stable nesting habitats (Westrich 1996) and are known to frequently move from their nests in search of floral resources (Klatt et al. 2020).

The complexity of the issue is further increased when considering the landscape context in which restoration measures are implemented (Tonietto & Larkin 2018; Sexton & Emery 2020). The effectiveness of restoration may depend on the complexity or heterogeneity (i.e. the extent and spatial distribution of land cover and land use categories) of the surrounding landscape (Concepción et al. 2008; Peralta et al. 2023). Landscape composition can influence the distribution of pollinator species across the landscape (Peralta et al. 2023) and modulate the presence and proximity of source populations of pollinators, namely, the regional species pool that may potentially colonize newly established or improved habitats (Woodcock et al. 2021). The interconnectedness between local restoration measures and broader landscape context underscores the importance of considering landscape-wide dynamics when evaluating restoration outcomes.

Research aimed at assessing the effects of restoration measures on pollinators has mostly focused on evaluating the diversity of pollinators in areas that have undergone restoration (Zamorano et al. 2020). Conversely, the effectiveness of restoration in enhancing pollinator richness and abundance in neighboring, unrestored areas has been less studied (Jönsson et al. 2015; Scheper et al. 2015). Cross-habitat fluxes of organisms represent a key process, exerting a substantial influence on wildlife populations within human-dominated landscapes, with the potential to shape landscape-wide community structure and associated processes. In this context, the assessment of potential beneficial effects of restoration measures on unrestored areas is of paramount importance, as it allows to evaluate whether locally restored habitats can lead to an improvement in pollinator communities at the landscape scale (Zamorano et al. 2020).

In this study, we investigated the effects of restoring seminatural habitats, in particular through the establishment of wildflower strips and species-rich grasslands, on pollinator communities on nine farms. Our analysis included both restored and adjacent unrestored areas to capture potential beneficial effects at a broader scale. To better understand potential differences in pollinator responses to habitat restoration resulting from differences in pollinator life-history traits such as resource requirements, mobility, and specialization in nesting and overwintering habitats, we compared the responses of bumblebees and butterflies. Specifically, we aimed to answer three questions: (1) How do butterflies and bumblebees differ in their response to the restoration of seminatural habitats, and what role do their different life-history traits and resource-use strategies play in mediating their responses? (2) To what extent do restored habitats influence pollinator communities in neighboring, unrestored areas, indicating broader beneficial effects? (3) How do differences in landscape composition influence the effectiveness of local habitat restoration in enhancing pollinator richness and abundance?

Methods

Study Area

The study was conducted on nine farms in the eastern Po Valley in Italy (see Fig. 1), a region heavily shaped by urban sprawl and intensive agricultural practices (Lorenzato et al. 2024). The study area has a subhumid continental climate with an average annual precipitation of 850 mm (Berti et al. 2014). The mean annual temperature ranges between 10 and 14.4°C. Average minimum temperature in the coldest month of the year (January) is −1.5°C, while the average maximum in the warmest month (July) is 27.2°C (Masin et al. 2010). The soils are predominantly silty clay, formed by the accumulation of alluvial material transported by the region's rivers (Regione Veneto 2005).

The farms were part of a large-scale European LIFE project (LIFE19 IT/NAT/000848 PollinAction; www.lifepollinaction.eu, accessed in May 2025). The project aimed to mitigate the ongoing pollination crisis (e.g. Potts et al. 2010) by increasing landscape heterogeneity through the establishment of a network of multifunctional natural and seminatural habitats. Strategic planning was informed by previous studies (e.g. Torchio et al. 2024) indicating that the most effective approach combines large habitat patches, which support the persistence of pollinator

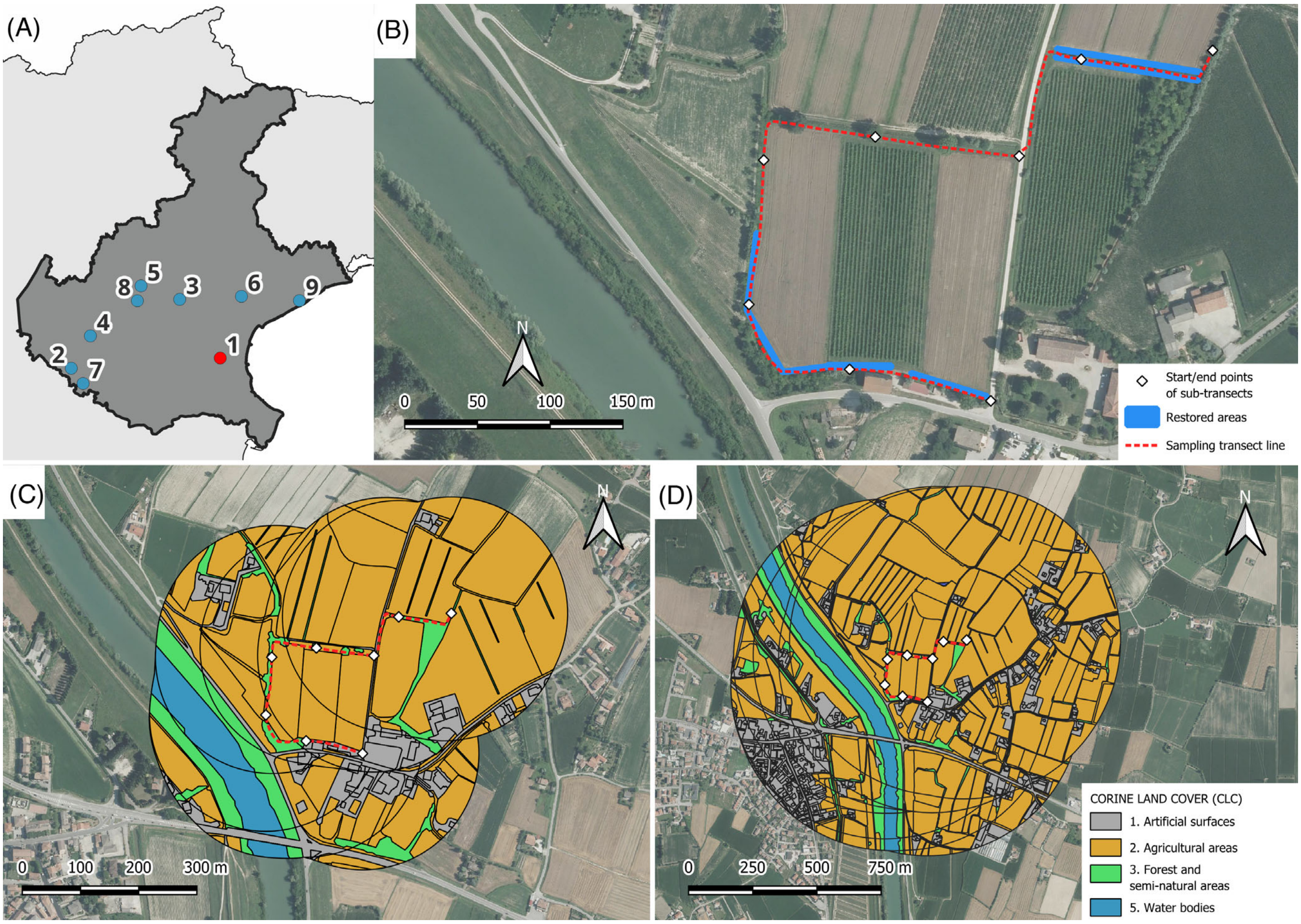

Figure 1. Study area and example of transect layout and landscape characterization. (A) Location of the nine study farms across the Veneto Region (Italy). (B) Example from Farm 1, showing the sampling transect (red line), its 100 m sub-transect start/end points (white diamonds), and restored areas (blue polygons). (C, D) Examples of the 200 m (local scale; C) and 600 m (landscape scale; D) buffers delineated around each sub-transect, illustrating the distribution of land cover/land use classes based on CORINE Land Cover (CLC): 1. "Artificial surfaces," 2. "Agricultural areas," 3. "Forest and seminatural areas," 5. "Water bodies."

populations, with smaller, spatially dispersed patches that ensure a continuous distribution of floral resources across the landscape. Habitat selection for restoration was guided by the key ecological requirements of pollinators, including access to nectar and pollen resources, the continuous availability of flowers during their active season, and the presence of suitable nesting and overwintering habitats. Based on these criteria, two primary habitat types were identified: wildflower strips and species-rich grasslands. Species-rich grasslands support a variety of pollinators due to their structural complexity and floral diversity, ensuring floral and nesting resources for pollinators with different requirements (e.g. Fantinato et al. 2019, 2021). Flower strips are small landscape elements that are typically established in orchard inter-rows and along field margins (Favarin et al. 2024). In line with the objectives of the Common Agricultural Policy Agri-Environmental Schemes, they are specifically designed to provide spatially and temporally heterogeneous floral resources throughout the pollinator activity period (Cano et al. 2022). Based on the considerations outlined above, the project included the establishment of species-rich grasslands with an average area of around 3.5 ha and flower strips with an average area of around 1500 m^2.

Restoration methods followed established best practices in ecological restoration (Török et al. 2011) and nature-based solutions, combining the planting of native herbaceous seedlings with the sowing of locally sourced seed mixtures to increase species richness and accelerate habitat establishment. Species were selected based on their ecological relevance, regional provenance, and suitability to pollinator needs. All propagation material was collected from wild plant populations located as close as possible to the restoration sites to preserve intraspecific genetic diversity (Höfner et al. 2022). Seed harvesting, carried out between late spring and early autumn in accordance with species phenology, was supplemented by controlled propagation in flowerbeds and production fields. In selecting species for both seed mixtures and plug plants, care was taken to maximize the diversity of floral traits (shape, size, color, and resources) while taking into account habitat-specific ecological requirements, local climate, and projected climate change impacts, prioritizing resilient, cost-effective species that can reliably establish on different soil types (Table S1). Particular attention was given to the use of native species due to their ecological compatibility with local environmental conditions and their co-evolutionary relationships with native pollinators (Burghardt et al. 2009). Horticultural or non-native species, commonly used in ornamental plantings, were excluded due to their potential to outcompete native flora and promote invasive dynamics and their capacity to disrupt foraging behavior, alter pollinator community composition, and affect the structure of plant-pollinator networks (Seitz et al. 2020).

Restoration measures took place on all farms from autumn 2021 to early spring 2022. Restoration measures involved the use of 95,734 native plug plants and 85.1 kg of locally sourced seed mixtures. Wildflower strips were typically established along field margins subject to intense disturbance from agricultural operations, either on bare ground or in vegetated areas generally dominated by grasses and a few scattered ruderal forbs. In contrast, species-rich meadows were created from former arable fields or by enriching intensive permanent grasslands, which were dominated by a few competitive grass species and managed by mechanical mowing for hay production.

Data Collection

Data collection focused on butterflies (Lepidoptera: Papilionoidea and Hesperioidea) and bumblebees (Hymenoptera: Apidae: *Bombus* spp.), as these groups are widely recognized as key pollinator indicators in monitoring programs (e.g. Potts et al. 2024) due to their ease of field identification and the extensive knowledge on their ecology and behavior (Amiet 1996; Paolucci 2010), and growing concern over their marked declines in recent decades (Habel et al. 2019; Vray et al. 2019).

A single sampling transect was established on each of the nine farms, ranging in length from 700 to 1000 m. Transects placement was designed to quantify the variation in butterfly and bumblebee communities before and after restoration, while accounting for within-farm landscape heterogeneity. In each sampled farm, a starting point was established within a restored area, and transects were then laid out along contrasting land cover/land use elements to ensure representative sampling of the farm landscape. All transects were georeferenced to record their exact location (Figs. 1 & S1). Each sampling transect was divided into 100-m sub-transects, which were then categorized as either restored or unrestored.

Standardized transect counts (Pollard & Yates 1993) were utilized to record the total number of butterfly and bumblebee species (as an indicator of species richness) and the total number of individuals (as an indicator of abundance) on the selected farms. A consistent walking pace was maintained along each transect, which was walked in a single direction, and all butterflies and bumblebees observed within a 5-m range ahead and 2.5 m on either side of the surveyor were identified and counted. When individuals could not be reliably identified in the field, they were captured using a butterfly net for subsequent identification to the species level following Paolucci (2010) for the butterflies and Falk (2019) and Amiet (1996) for the bumblebees. The total time spent sampling all transects across the nine farms was approximately 68 hours. Surveys were conducted once per month, from May to September, ensuring coverage of the flight periods of butterflies and bumblebees. The surveys were conducted under specific weather conditions, with temperatures above 13°C in sunny weather and 17°C in overcast conditions, and with wind speed not exceeding four on the Beaufort scale (Pollard & Yates 1993). Standardized transect counts began in 2022, coinciding with the completion of the restoration works. Since the planted seedlings and the seed mixtures consisted of perennial species, which typically do not flower during their first growing season after establishment, monitoring carried out in 2022 was considered to represent the pre-restoration (ex ante) condition. The survey was repeated in 2023 representing the post-restoration (ex post) situation. It is established that herbaceous vegetation often improves significantly within a year of restoration, which can significantly support pollinators (e.g. Hofmann & Renner 2020).

The landscape context along each 100 m sub-transect was assessed using a high-resolution land cover map based on aerial photographs provided by the Veneto Region (resolution: 0.2 m × 0.2 m) in QGIS 3.28.15 (QGIS Development Team 2025). Considering that different spatial scales can reveal different effects on environmental processes (Lindborg et al. 2017), we identified two extents (i.e. buffers) at which to evaluate the effects of habitat restoration on butterfly and bumblebee communities: 200 m buffer (local scale) and 600 m buffer (landscape scale). Buffers were generated in a Geographic Information System environment using the *buffer* function. Buffer shapes were defined by the shape of each sub-transect from which they were created. In each sub-transect and for each buffer, all landscape elements identifiable at a scale of 1:500 were drawn and categorized according to the CORINE Land Cover (CLC) classification at level 3 (Bossard et al. 2000). The land cover/land use types were then grouped into CLC macro-categories (1. "Artificial surfaces," 2. "Agricultural areas," 3. "Forest and seminatural areas," 5. "Water bodies") prior to the calculation of their percent cover in each map. Ditches, drains and banks characterized by the presence of native herbaceous vegetation were included in macro-category 3. "Forest and seminatural areas" due to their provision of essential resources for butterflies and bumblebees, including food, refuge and nesting sites (An & Choi 2021; Twerd et al. 2022). Large inland water bodies (macro-category 5. "Water bodies", e.g. artificial water drainage channels, rivers and lakes) were mapped and quantified; however, although their extent was recorded, they were excluded from further analyses due to the overall low percentage of cover (Tables S2 & S3).

Data Analysis

To assess sampling completeness, species accumulation curves were calculated for butterfly and bumblebee communities for each farm and each sampled year (i.e. 2022 and 2023) using the specaccum function (package vegan, version 2.6-8). For each farm and year combination, species richness was expressed as a function of the number of sub-transects sampled.

To investigate the effect of restoration measures on butterfly and bumblebee communities across the two sampling years (2022 and 2023), we calculated, for each sub-transect and each monthly survey, the difference in species richness and abundance between the 2 years (2023–2022). Restoration status (restored vs. unrestored sub-transects) was included as a categorical variable. To distinguish between the two categories, we used an empirical threshold derived from the bimodal distribution of the percentage of restored area. The local minimum in the density function (39.57%) was used to define the cut-off, resulting in two clearly distinguishable groups: restored (≥39.57% of the sub-transect length traversing restored area; $n = 39$) and unrestored sub-transects (<39.57% of the sub-transect length traversing unrestored area; $n = 30$) (Fig. S2). Landscape composition was characterized by the percent cover of urban areas, agricultural land, seminatural areas, and restored areas, with all land cover predictors centered (mean = 0). To assess the influence of the percent cover of restored area and of landscape composition (i.e. urban, agricultural land, and seminatural areas, hereafter land cover/land use types) on the variation in species richness and abundance of butterflies and bumblebees, we fitted eight linear mixed models (LMMs). Specifically, we modeled four response variables (i.e. changes in butterfly abundance [ΔBA], butterfly species richness [ΔBSR], bumblebee abundance [ΔBBA], and bumblebee species richness [ΔBBSR]), each analyzed at two spatial extents (i.e. 200 and 600 m). Each model included restoration status (restored vs. unrestored) and the percent cover of restored area and of land cover/land use types (i.e. agricultural land and seminatural areas) as fixed effects, along with their two-way interactions, to test whether the effect of landscape composition differed between restored and unrestored sub-transects. Collinearity among predictors was assessed using Spearman test, and only linearly independent variables were retained ($r < 0.7$) (Fig. S3). Due to the association between urban and agricultural land cover across both buffer extents, and because the farms were embedded in predominantly agricultural contexts, urban cover was excluded from the models. Normality of residuals and homoscedasticity were visually inspected in R and determined to meet model assumptions in all cases. Individual surveys were treated as replicates, with farm and sub-transect identities included as random factors in the models. Using a stepwise backward selection procedure, we sequentially removed the least significant variables and interactions from the model at each step until only predictors with p less than 0.05 were retained. All models were generated using R version 4.2.2 with lme4 package (lmer function; R Core Team 2022).

Results

During the 2-year sampling period, a total of 32 butterfly species with 2451 individuals, and nine bumblebee species with 493 individuals were recorded. The most common butterfly species was *Polyommatus icarus* (423 individuals), followed by *Pieris brassicae* (420 individuals) and *P. rapae* (397 individuals) (see Table S4). Among the bumblebees, the most abundant species was *Bombus pascuorum* (272 individuals), followed by *B. terrestris* (136 individuals) and *B. hortorum* (46 individuals) (Table S4). For both butterflies and bumblebees, the species pool was dominated by generalist species (94 and 67% of observations, respectively).

Overall, species accumulation curves for both butterflies and bumblebees indicated that the sampling effort was generally sufficient to capture local species richness across the nine farms (Fig. S4). Most species accumulation curves reached an asymptote, indicating that most species on each farm were detected. For butterflies, accumulated richness was higher in 2023 than in 2022, with species accumulation curves above those from 2022. For bumblebees, despite the lower overall number of species and greater variability between farms, a similar trend was observed.

The abundance of individuals of both pollinator groups increased between 2022 and 2023 (Table 1), whereas species richness remained relatively stable, often showing only species turnover between sampling years (Tables 1 & S4).

When considering the difference in species richness and abundance between 2023 and 2022, the two groups of pollinators exhibited divergent results, with butterflies being more sensitive to restoration measures than bumblebees. Across all sub-transects (i.e. both restored and unrestored), the proportion of positive responses of butterflies (i.e. increase in species richness or abundance) was 54.15 and 68.48% for species richness and abundance, respectively. In contrast, species richness for bumblebees increased in only 47.56% of transects and positive responses for abundance fell to 37.82%, with neutral responses (i.e. no change) forming the majority (54.15%). Comparable results were observed when assessing sub-transects over restored areas, with species richness and abundance of butterflies increasing in 56.12 and 68.37% of sub-transects, respectively. For bumblebees, species richness increased in only

Table 1. Total species richness and abundance of butterflies and bumblebees recorded during the two sampling years (2022 and 2023). Values are reported separately for trophic generalist and specialist species. The classification followed Öckinger et al. (2010) for butterflies and Goulson et al. (2005) for bumblebees (see Table S4).

		2022		2023	
Pollinator group	*Dep. variable*	*Generalist*	*Specialist*	*Generalist*	*Specialist*
Butterfly	Species richness	28	2	27	1
	Abundance	760	32	1687	37
Bumblebee	Species richness	5	1	5	3
	Abundance	104	3	365	48

9.18% of restored sub-transects, while abundance increased in only 40.81% of sub-transects, with neutral responses observed in 42.37 and 51.02% of sub-transects, respectively. In unrestored sub-transects, butterflies responded positively overall (with an increase in species richness and abundance in 52.34 and 69.80%, respectively), while the increase in species richness for bumblebees was observed in only 10.07% of sub-transects and in 34.90% when considering abundance. Moreover, the neutral responses were higher than positive ones (42.95% for species richness, and 57.72% for abundance).

At all investigated buffers, the surrounding landscape was dominated by agricultural land (on average, 200 m buffer: 76.24 ± 13.97%; 600 m buffer: 74.72 ± 11.15%). The coverage of forest and seminatural areas varied markedly, ranging from 2.45% to 23.43%, with an average of 6.53% ± 3.63% within the 200 m buffer and 8.35% ± 5.73% within the 600 m buffer. The percent cover of restored areas ranged from 0.25 to 3.40% within the 200 m buffer, decreasing to 0.03 and 0.44% within the 600 m buffer.

The influence of percent cover of restored area and of land cover/land use types on pollinator responses varied between the different pollinator taxa (butterflies vs. bumblebees), between the different sub-transect types (restored vs. unrestored), as well as at different spatial scales (200 and 600 m buffers), as summarized in Table 2.

At the local scale (i.e. 200 m buffer), both species richness and abundance of butterflies were significantly and positively influenced by the percent cover of restored area (Table 2; Fig. 2). Specifically, positive changes in butterfly richness (ΔBSR) were associated with increasing percent cover of restored areas, indicating that restoration measures significantly contributed to an enhancement in species richness between 2022 and 2023 (Table 2; Fig. 2A). Similarly, butterfly abundance (ΔBA) responded positively to the proportion of restored area, with higher percent cover of restored area associated with larger increases in abundance between years (Table 2; Fig. 2B). No significant effects of other land cover/land use types were observed at this spatial scale.

At the landscape scale (i.e. 600 m buffer), changes in butterfly richness (ΔBSR) were significantly influenced by the interaction between restoration status and landscape composition (i.e. percent cover of restored area and of land cover/land use types), whereas ΔBA were only affected by the percent cover of restored area (Table 2; Fig. 3). In restored sub-transects, butterfly species richness increased with the percent cover of restored area, while in unrestored sub-transects no significant relationship was observed (Table 2; Fig. 3A). Similarly, the effects of agricultural and seminatural land cover differed depending on restoration status: in unrestored sub-transects, butterfly richness tended to increase with increasing cover of these land cover/land use types (Table 2; Fig. 3B & 3C), whereas in restored sub-transects the same variables had no or negative effects. Butterfly abundance (ΔBA) at the 600 m scale was positively associated with the percent cover of restored areas regardless of restoration status, and no significant effect of percent cover or land cover/land use types was detected (Table 2; Fig. 3D). For bumblebees, neither restoration status nor the percent cover or land cover/land use types significantly influenced changes in species richness (ΔBBSR) or abundance (ΔBBA) at either the local (200 m) or landscape (600 m) scale.

Discussion

In line with previous research (e.g. Cariveau et al. 2020; Sexton & Emery 2020), our study confirms that habitat restoration in intensively managed agricultural landscapes can support pollinator communities. Since plants and pollinators share a mutualistic relationship, the increase in plant species richness and abundance resulting from habitat restoration efforts provides additional resources and habitat niches, supporting a greater

Table 2. Statistical summary of results of changes in butterfly species richness (ΔBSR) and abundance (ΔBA) in relation to restoration status, percent cover of restored area, agricultural land, and seminatural area, and their interactions with restoration status (i.e. restoration status × % restored area, restoration status × % agricultural land, restoration status × % seminatural area). Results are reported separately for 200 m (local scale) and 600 m (landscape scale) buffers. Chi-square (χ^2) values are reported for fixed effects only; intercepts are shown with their estimate, SE, *t*-value, and *p* value.

Response variable	*Fixed effect*	*Est. coeff.*	*SE*	Z-score	p	χ^2	*Significance*
200 m buffers							
ΔBSR	Intercept	0.836	0.124	6.752	<0.001	—	***
ΔBSR	% Restored area	0.399	0.123	3.237	0.002	10.480	**
ΔBA	Intercept	2.639	0.356	7.407	<0.001	—	***
ΔBA	% Restored area	1.179	0.357	3.298	0.002	10.878	**
600 m buffers							
ΔBSR	Intercept	0.736	0.122	5.990	<0.001	—	***
ΔBSR	Restoration status	0.352	0.181	1.945	0.052	3.784	
ΔBSR	% Agricultural land	0.013	0.020	0.669	0.319	1.081	
ΔBSR	% Seminatural area	0.059	0.039	1.512	0.683	0.177	
ΔBSR	% Restored area	1.739	1.283	1.356	0.007	11.690	**
ΔBSR	Restoration status × % agricultural land	−0.065	0.030	−2.142	0.033	4.587	*
ΔBSR	Restoration status × % seminatural area	−0.145	0.053	−2.717	0.007	7.381	**
ΔBSR	Restoration status × % restored area	4.247	1.854	2.290	0.023	5.247	*
ΔBA	Intercept	2.644	0.390	6.785	<0.001	—	***
ΔBA	% Restored area	8.225	3.406	2.415	0.041	5.831	*

Significance: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

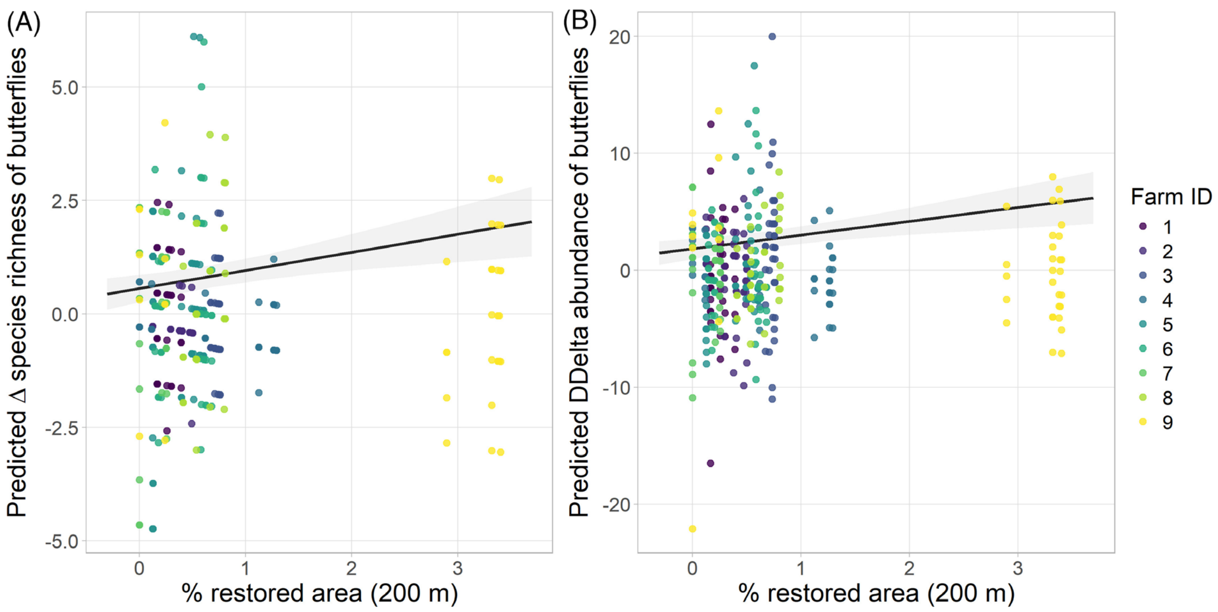

Figure 2. Visualization of the partial effects of linear mixed models (LMMs). Points represent partial residuals colored by farm identity (Farm ID, as reported in Fig. 1), regression lines represent predicted effects, and colored bands indicate 95% CIs.

diversity of pollinators (Kral-O'Brien et al. 2021). The relationship between plants and pollinators is so tight that Curtis et al. (2015) suggested that pollinator population carrying capacity, particularly for butterflies, could be predicted based on plant community composition.

However, in the present study, the effects of habitat restoration differed between the two target pollinator groups. Butterfly populations responded positively, with both species richness and abundance significantly increasing in response to restoration. In contrast, bumblebee species richness and abundance showed no statistically significant responses, although descriptive trends suggested potential local improvements. Our results are consistent with previous findings which also reported weak or variable bumblebee responses to restoration efforts (e.g. Redhead et al. 2016; Timberlake et al. 2020). The discrepancy between butterfly and bumblebee responses likely reflects differences in resource requirements, mobility and specialization in nesting and overwintering habitats between the two groups. Bumblebees are known for their ability to rapidly colonize newly available habitats (Alanen et al. 2011; Öckinger et al. 2018), and for their capacity to disperse over large distances in search of food resources (Westphal et al. 2006; Rao et al. 2019). However, in temperate regions, the majority of bumblebees are considered central foragers (Polidori et al. 2025), meaning that their foraging activities are spatially constrained by the location of their nesting site, with foraging range largely dictated by flight capabilities (Gathmann & Tscharntke 2002). The energetic cost of commuting between nesting and foraging sites can be substantial (Favarin et al. 2022) and may explain their neutral response to the percent cover of restored areas. Moreover, short-term increases in floral resources following habitat restoration can enhance worker and male numbers, though such effects may not immediately lead to increased reproductive output (Williams et al. 2012). Finally, population patterns observed could reflect processes such as dilution, spillover, or local concentration of individuals (Kleijn et al. 2019).

The contrasting responses we observed between butterflies and bumblebees support the value of butterflies as sensitive bioindicators of habitat quality and landscape change, offering a robust, cost-effective proxy for broader biodiversity patterns (see, e.g. the Butterfly Index; Van Swaay et al. 2015; Potts et al. 2024). Unlike bumblebees, whose high mobility and foraging behavior may allow them to utilize resources across larger areas (Vieli et al. 2016), butterflies often exhibit narrower ecological requirements and may be more influenced by local habitat conditions, such as plant composition, fragmentation, or microclimatic conditions (Menéndez et al. 2007). Because butterflies respond to both local habitat conditions and broader landscape-scale changes, they provide a multiscale perspective that is particularly useful in assessing the effectiveness of restoration interventions (Shuey et al. 2017).

The positive responses we observed were driven mainly by generalist taxa, such as Pieridae and Lycaenidae, which are abundant in the study farms, a pattern consistent with previous research showing that restoration in intensively managed landscapes tends to favor mobile or generalist species over specialists (e.g. Komonen et al. 2004; Börschig et al. 2013). The composition of the regional species pool is likely a crucial factor in determining which species can successfully colonize restored areas. Our study region, shaped by urban sprawl and agricultural intensification (Lorenzato et al. 2024), likely hosts a depleted regional species pool, where specialists are rare due to the scarcity of specific larval host plants

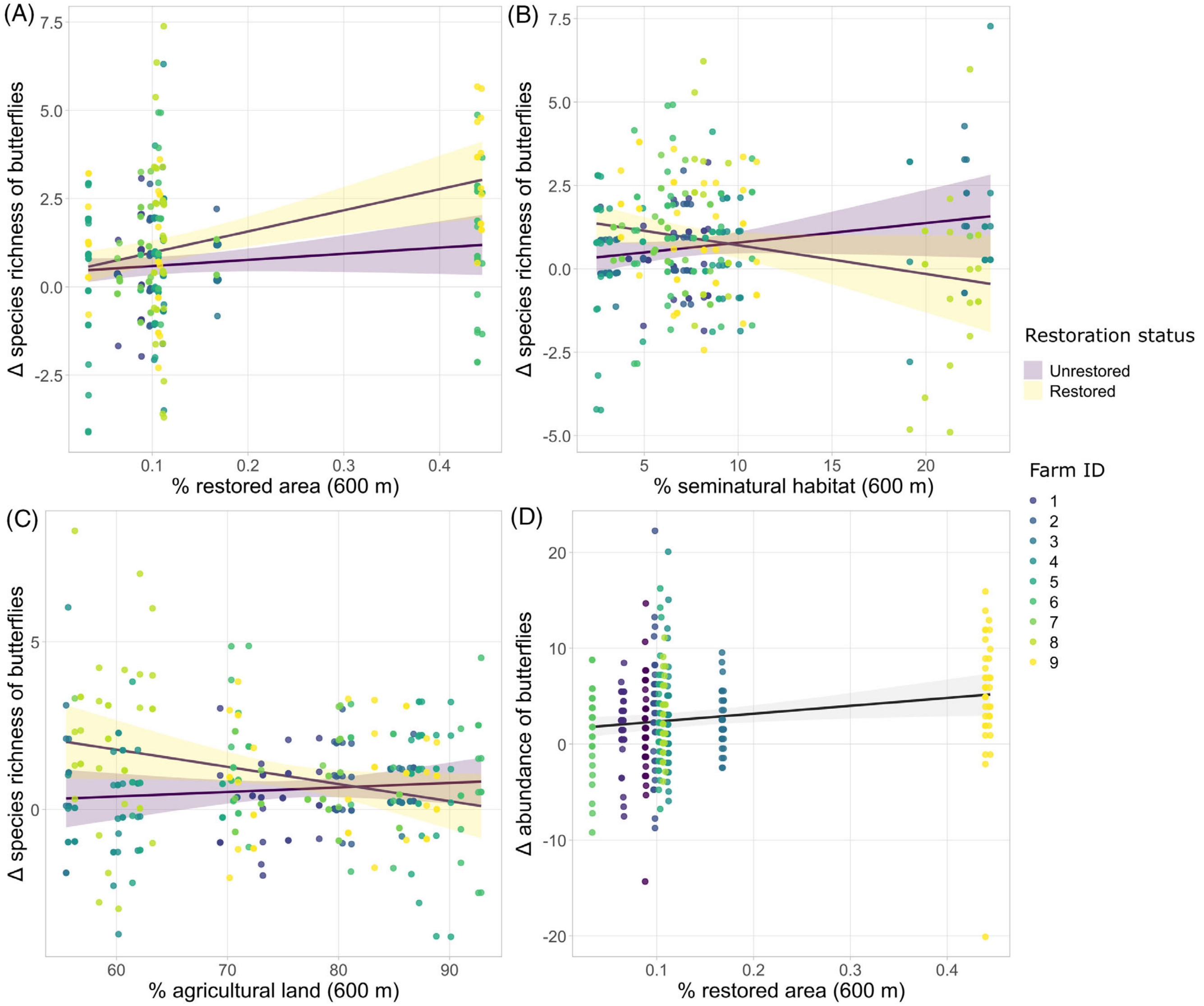

Figure 3. Visualization of the partial effects of linear mixed models (LMMs). Points represent partial residuals colored by farm identity (Farm ID, as reported in Fig. 1), regression lines represent predicted effects, and colored bands indicate 95% CIs.

or suitable nectar-producing plants and microhabitats (Öckinger et al. 2010; Curtis et al. 2015). However, since specialists were scarce in the studied farms, it is not possible to draw sound conclusions regarding their response to restoration.

Our data also indicate that restored areas may exert positive effects on nearby unrestored areas; namely, restored areas not only serve as concentration zones for pollinator species and individuals but also provide additional foraging and nesting habitat that can benefit populations in nearby unrestored areas. In our study, both restored and unrestored sub-transects at the local scale (200 m) showed increases in species richness and abundance with increasing proportions of restored areas in the surrounding landscape, suggesting that landscape composition likely modulates the influence of restoration efforts, and supporting the importance of spatial proximity in facilitating pollinator movement (Viana et al. 2012).

The importance of spatial scale emerged as a recurring theme in our study, underscoring that the interaction between restored habitats and the surrounding landscape context operates across multiple spatial scales, likely by affecting the availability of complementary resources and source populations (Montoya et al. 2012). Interestingly, although butterflies responded positively to restoration at both local and landscape scales, the mechanisms underlying the response differed: while at the local scale (200 m) the percent cover of restored habitat was the only significant variable, at the landscape scale (600 m), butterfly responses showed a more complex pattern, especially regarding species richness. In particular, changes in abundance followed a pattern similar to that observed at the local scale, while variations in species richness were clearly influenced by interactions with surrounding land cover/land use types (agricultural and seminatural areas), confirming the importance of landscape context, particularly in unrestored sub-transect. In this context, agricultural areas themselves contribute to pollinator richness, as synanthropic generalist butterfly species (e.g. Pieridae) can exploit cultivated areas and ruderal field margins as alternative habitats (Harvey & Wagenaar 2006). Synanthropic generalist species perceive the agricultural matrix as less hostile compared to specialist taxa, which are often more sensitive to habitat degradation (e.g. Tscharntke et al. 2012), highlighting that even agricultural landscapes may contribute to pollinator movement and persistence in ways that depend on species-specific traits and functional group characteristics (Hass et al. 2018). Such ecological responses may help explain the negative relationship observed between the increase in species richness and the percent cover of agricultural and seminatural areas in restored sub-transects: generalist butterfly species (e.g. Pieridae) can exploit floral resources and habitat niches available in agricultural fields and margins, thereby reducing their dependence on restored patches (Rundlöf et al. 2008). At the same time, in landscapes already rich in seminatural habitats, the incremental contribution of restored patches may be limited, as local communities are likely saturated and the potential for further increases in species richness is reduced (Tscharntke et al. 2012).

In conclusion, our study supports the value of butterflies as sensitive indicators of habitat quality and restoration outcomes, as they respond consistently to both local and landscape-scale changes in habitat structure and composition. In addition, compared to other insect groups, butterflies benefit from a well-resolved taxonomy in which most species are already described and identifiable, as well as an extensive ecological literature detailing their habitat requirements, host plants, and life-history traits.

Our findings can inform the implementation of the new European Union (EU) Restoration Law (European Union 2024), which calls for the establishment of standardized monitoring schemes to track pollinator abundance and diversity by 2025. They are also in line with the first objective of the revised EU Pollinators Initiative (European Commission 2023), which emphasizes the development of systematic monitoring systems, an approach in which butterflies represent a scientifically robust and cost-effective indicator group due to their ecological specificities and responsiveness to environmental change.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Overview of the nine study farms included in the survey.
Figure S2. Distribution of the percentage of restored area within sub-transects across all sampled farms.
Figure S3. Correlation matrices among predictors at 200 m (a) and 600 m (b).
Figure S4. Species accumulation curves for butterfly (a) and bumblebee (b) communities sampled across all study farms in 2022 and 2023.
Table S1. List of species used in restoration measures.
Table S2. Land cover and land use macro-categories and CORINE Land Cover classes mapped inside landscape buffers.
Table S3. Mean percentage (%) and standard deviation of CLC classes and restored area within analyzed buffers (200 and 600 m) for each sampled farm.
Table S4. Abundance of butterfly and bumblebee species recorded in the two sampling years across the nine farms.

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