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Ecological Intensification as a pathway to support semi- natural habitats and arthropod functional groups in agriculture

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Abstract

In recent decades, agricultural intensification has led to the loss of agricultural biodiversity and many semi-natural habitats in Europe. The loss of important semi-natural habitats has compromised agroecosystems and their associated ecosystem services.

Two of the most important ecosystem services are pest control and pollination, both provided by beneficial arthropod functional groups: pollinators and natural enemies (i.e. predators and parasitoids). Beneficial functional groups of arthropods are supported in the agricultural landscape by various semi-natural habitats such as flower strips, meadows and hedgerows. Ecological intensification aims to restore and conserve these important semi-natural habitats to support beneficial functional groups of arthropods for associated ecosystem services. By studying the structure and composition of plant communities, the landscape context and the management of these semi-natural habitats, this thesis aims to investigate how conservation and restoration practices can support and foster associated beneficial arthropod communities.

The thesis results show that ecological intensification practices for restoring and conserving these semi-natural habitats benefit functional groups of arthropods, reinforcing their critical role in sustainable agriculture. The following thesis provides practical insights for improving plant and arthropod communities in intensive agricultural landscapes by integrating biodiversity-friendly agricultural practices.

Negli ultimi decenni, l'intensificazione dell'agricoltura ha portato alla perdita della biodiversità agricola e di molteplici habitat seminaturali compromettendo gli agroecosistemi e i servizi ecosistemici ad essi associati.

Due servizi ecosistemici importanti in agricoltura sono il controllo dei parassiti e l'impollinazione, forniti da gruppi funzionali di artropodi benefici: gli impollinatori e i nemici naturali (i.e. predatori e parassitoidi). Questi gruppi funzionali beneficiano di vari habitat seminaturali presenti nel paesaggio agricolo, come le strisce fiorite, i prati da sfalcio e le siepi. L'intensificazione ecologica mira a ripristinare e conservare gli habitat seminaturali per favorire i gruppi funzionali di artropodi e migliorare i servizi ecosistemici associati. Studiando la struttura e la composizione delle comunità vegetali, il contesto paesaggistico e la gestione degli habitat seminaturali, questa tesi si propone di indagare come le pratiche di conservazione e ripristino ecologico possano promuovere le comunità di artropodi benefici ad essi associati.

I risultati della tesi mostrano che le pratiche di intensificazione ecologica favoriscono i gruppi funzionali di artropodi benefici rafforzando il loro ruolo nell'agricoltura sostenibile. La tesi fornisce spunti pratici per migliorare le comunità di piante e artropodi in un contesto di paesaggio agricolo intensivo, integrando pratiche agricole favorevoli alla conservazione della biodiversità.

Chapter 1

Introduction

Agricultural intensification and Ecological intensification

Since the second half of the 19th century, agriculture has undergone a profound transformation, largely driven by the principles of the Green Revolution approach (Hazell, 2008), which have led to a significant intensification of agricultural practices (Pretty, 2008). This shift was primarily induced by the need to increase food and fibre production to meet the demands of a growing population (L. T. Evans, 2003). The adoption of machinery, technology, agrochemicals (such as herbicides and pesticides) along with financial investments has led to the standardisation of agricultural practices, that however has come at the cost of reduced crop diversity and the abandonment of traditional farming practices (Emmerson et al., 2016). While the intensification process boosted productivity, it has also led to a range of environmental and ecological drawbacks it also generated numerous negative externalities, including the depletion of soil fertility, pollution, an increase in pest populations, increased resistance to pesticides, as well as a general simplification of agricultural landscapes, resulting in marked decline in biodiversity (Tilman et al., 2002) and the ecosystem services it sustains, with pollination and biological pest control being among the most at risk. To address the increasingly negative effects of agricultural intensification, a new agricultural model, known as “agricultural sustainable intensification”, was proposed in the 1980s (Godfray et al., 2010; Rockström et al., 2017). Sustainable intensification of agriculture aims to increase productivity while preserving the resilience of agricultural systems. This approach employs various methods to maintain natural resources during production (Kassie et al., 2015) and has increasingly become a central focus in global development agendas and is recognized as a key strategy in the United Nations Sustainable Development Goals (SDGs), contributing to the achievement of ‘Zero Hunger’ (SDG2) and the sustainable use of terrestrial ecosystems (SDG15) (Godfray et al., 2010; Rockström et al., 2017). However, the recognition that the loss and fragmentation of natural and semi-natural habitats within agricultural landscapes represent major drivers of biodiversity and functional decline (Benton et al., 2003; Robinson & Sutherland, 2002; Tilman et al., 2002) has prompted the suggestion of alternative approaches, such as the ‘ecological intensification’. Ecological intensification focuses on replacing external inputs with ecological processes and biological functions (Petersen & Snapp, 2015) and aims to maximise ecosystem services through the efficient use and preservation of natural resources (Xie et al., 2019). Ecological intensification has been proposed as a nature-based alternative that integrates (or partially replaces) external inputs, such as pesticides, with ecological processes that support agricultural production while minimizing negative environmental impacts (Kleijn et al., 2019). This approach is based on the premise that in conventional intensive farming systems (characterized by high external inputs) ecosystem service provision is suboptimal and that managing specific components of biodiversity (e.g., semi-natural habitats) can help supplement or replace artificial inputs, thereby reducing environmental costs without compromising productivity.

The European perspective

Agriculture is one of the most predominant land uses in Europe, covering approximately 38% of the total land area (Eurostat 2020). Historically, agricultural landscapes, characterised by a great diversity of semi-natural habitats and a wide variety of different crops, supported high levels of biodiversity (Bignal & McCracken,

1996). Low-intensity farming practices, in the form of livestock rearing and traditional cultivation methods, created semi-natural habitats (hedgerows, species-rich grasslands and hay meadows, woodland patches, and channels), that played a crucial role in supporting a wide range of species and ensuring ecological stability (Tscharntke et al., 2005). In Europe, agricultural intensification resulted from a multifactorial process mainly aimed at increasing per hectare unitary productivity (Donald et al., 2006; Herzog et al., 2006; Matson et al., 1997). The Common Agricultural Policy (CAP), developed from 1962 to 1992, was crucial in promoting the intensification and mechanisation of European agriculture (Gay, 2005). Specifically, agricultural intensification has been driven by two processes, operating at distinct spatial scales (Emmerson et al., 2016). At the field level, the intensification of management practices, characterised by increased agrochemicals and fertiliser inputs per unit of soil, as well as more intensive agricultural practices (e.g., ploughing, refining), has significantly contributed to soil degradation. At the landscape level, the simplification and homogenisation of agricultural systems marked by field enlargement, crop specialisation, the abandonment of crop rotation and a reduction in crop diversity have profoundly altered agroecosystems. In particular, field enlargement and landscape simplification have led to the decline of small marginal non-cultivated areas (Emmerson et al., 2016), and, in turn, to the loss of semi-natural habitats and the reduction in plant species richness, that play a crucial role in supporting biodiversity, providing essential food resources and refuge for many organisms (Emmerson et al., 2016). Thus, the loss of plant species induces radical shifts in the entire community of organisms, triggering a cascade effect across higher trophic levels: from primary consumers (i.e., herbivorous), secondary consumers (i.e., predator and parasitoids) to decomposers (i.e., detritivores and saprophages) (Ebeling et al., 2014; Gagic et al., 2014; Haddad et al., 2009). In turn, the reduction of biodiversity has effects on the reduction of associated ecosystem processes. Processes such as soil conservation, decomposition of organic matter, nutrient recycling (J. M. Holland et al., 2017), pollination (Garibaldi et al., 2011) and biological pest control (Östman et al., 2001, 2003; Thies & Tscharntke, 1999) are processes and services associated with plant and animal communities (Francis et al., 2021).

To address these challenges, recent European strategies such as the Green New Deal have introduced policies to align agriculture with biodiversity conservation goals. Policies such as the ‘Farm to fork strategy’ (EC, 2020a) and the ‘EU biodiversity strategy for 2030’ (EC, 2020b) have raised ambitious sustainability goals for agriculture and food systems. Agri-Environmental Schemes typically pursue multiple objectives, including nature conservation and resource protection. They focus on reducing external inputs, adopting organic and agroecological practices, and conserving or restoring semi-natural habitats such as hedgerows, small woodlands, ponds, wetlands, and field borders (Emmerson et al., 2016).

Ecosystem Services: the importance of pollination and pest control

The primary purpose of agriculture is to produce food, fibres, and other resources from plants and animals. Nevertheless, it is widely acknowledged that agricultural landscapes also provide a variety of other essential services, including regulating and supporting functions (MEA, 2005), that underpin crop production (Zhang et al., 2007). Ecosystem services such as soil fertility and nutrient cycling (Paul & Clark, 1996), water provisioning and purification (Eldridge & Freudenberger, 2005), crop pollination (Losey & Vaughan, 2006),

gene flow, and pest control (Naylor & Ehrlich, 1997) are fundamental to sustain agriculture's provisioning services (Zhang et al., 2007). As in other ecosystems, biodiversity, including genetic, species and habitat diversity, plays a vital role in ensuring the delivery of ecosystem services in agricultural settings (Moonen & Bàrberi, 2008). In particular, agricultural landscapes with greater diversity and a broader extent of semi-natural habitats support a wider range and higher quality of ecosystem services compared to those with lower diversity (García-Feced et al., 2015).

Pollination and pest control regulation are vital regulating ecosystem services in agricultural systems as they directly influence both the quantity and quality of numerous crop yields (Sutter & Albrecht, 2016). Animal pollination is a key service, supporting over 75% of the most important crops for human consumption and contributing to 35% of global food production (Klein et al., 2007). In temperate regions, the principal pollinators are insects (Kevan et al., 1990), with many economically valuable crops and fruit trees, such as apples and pears, relying on insect pollination (Abrol, 2012). While hymenopterans, in particular bees, are the most well-known pollinators, numerous other taxa, including dipterans, lepidopterans, coleopterans, also are important pollinators of both wild and crop plants (Rader et al., 2016). For example, wild bees have been shown to be more efficient pollinators compared to managed honeybees in apple orchards (Vicens & Bosch, 2000). Overall, higher richness of pollinator species is usually associated with increased pollination efficiency, leading to higher yields and greater stability of the pollination service. For example, Pisanty et al. (2016) found that greater richness of pollinator species enhanced pollination efficiency in watermelon plantations, a pattern similarly observed in blueberry crops (Rogers et al., 2014).

The ecosystem service of pest control and regulation also directly influences crop yield and quality. The presence of 'natural enemies', namely parasitoids and predators, provides a crucial biological mechanism, helping to suppress pest populations and mitigate possible outbreaks (Opender & Dhaliwal, 2003). Although often underappreciated, the economic value of this service is estimated to be worth billions of dollars annually on a global scale (Naranjo et al., 2015). The impact of agricultural industrialisation and the resulting landscape simplification has been particularly severe on animal pollination and natural pest control, as these services depend on mobile organisms that require natural and semi-natural habitats to complete their life cycles (Park et al., 2015; Rusch et al., 2016). Intensive agricultural areas are largely unsuitable for mobile arthropods due to landscape simplification and homogenisation and the extreme disturbance they are subjected to (Tscharntke et al., 2012). It is therefore essential to develop tools and models to guide the transition of the primary sector toward sustainable systems that can support production and business competitiveness while ensuring efficient resource use and enhancing the ecological quality underpinning the multifunctionality of agroecosystems (Landis et al., 2000). In line with the principles of Ecological Intensification, the creation or restoration of semi-natural habitats near croplands can offer alternative floral resources (e.g., nectar and pollen) along with shelter and nesting sites for various pollinator taxa (Eeraerts et al., 2021). Likewise, these habitats provide essential resources for natural enemies by supplying refuge, mating and overwintering sites, alternative hosts and prey, as well as additional trophic resources such as pollen and nectar (J. Holland et al., 2020; Landis et al., 2000).

Semi-natural habitats into intensive agricultural landscape

Numerous studies worldwide clearly demonstrate that agricultural intensification drives landscape simplification and biodiversity loss. The loss of biodiversity is threatening agricultural production, as essential ecosystem services that sustain crop yields are directly linked to biodiversity (Ismahane, 2024). However, for species to persist, forage, nest, reproduce, and hibernate, suitable habitats are required (Lundin et al., 2019; Sidhu & Joshi, 2016). In line with this principle, agri-environmental schemes (AES) have been implemented in the European Union to counter biodiversity decline, restore functional diversity, and enhance ecosystem services such as pollination and pest control within agricultural landscapes (Batáry et al., 2015). In agricultural landscapes, various habitats, such as hedgerows, flower strips, or species-rich meadows, can be created or restored to support species that provide essential ecosystem services (Sutter et al., 2018). However, significant knowledge gaps persist, particularly regarding habitat attributes, ecological interactions, and the long-term dynamics of these organisms (Tschardt et al., 2005). Additionally, a deeper understanding of landscape-scale management strategies is crucial for the effective implementation of ecological intensification (Kleijn et al., 2019). Bridging these gaps is essential for developing targeted conservation strategies and maximizing the benefits of ecosystem services in sustainable agriculture.

Managed field edges and flower strips are among the most common semi-natural habitats in European agricultural landscapes. These linear features, typically ranging from a few decimetres to several meters in width, consist of herbaceous vegetation restored and preserved along fields margins (Kowalska et al., 2022). They can be annual or perennial, and, in this latter case, they are managed through scheduled mowing to optimise floral resource availability (Nichols et al., 2022). To enhance their ecological benefits, various studies recommend the use of native plant species to support local biodiversity (Schmidt et al., 2020). Flower strips attract and support populations of beneficial insect, including pollinators and natural predators, facilitating their spillover into adjacent cultivated fields (Feltham et al., 2015). This process promotes the dispersal of predators and parasitoids within crops, contributing to biological control and reducing pest-related damage (Pywell et al., 2015). Both intrinsic factors, such as plant community composition (Blümel et al., 2024), and extrinsic factors, such as management practices (Piqueray et al., 2019), influence the communities of pollinators and natural enemies associated with these habitats. Additionally, the age of flower strips plays a role in shaping arthropod assemblages, favouring certain groups over others (Albrecht et al., 2021; Peer et al., 2024). Despite their widespread implementation, the effectiveness of these semi-natural habitats still needs further research (Zamorano et al., 2020). While numerous studies have demonstrated their role in attracting and supporting beneficial arthropods (e.g., Amy et al., 2018, Hatt et al., 2017), their effectiveness on pollination efficiency, pest control, and crop damage reduction is still debated (J. M. Holland et al., 2017; Lundin et al., 2023).

Similar to flower strips, managed interrows in orchards provide resources for pollinators and natural enemies (Abrol, 2012). Increasing the diversity of wild pollinators in orchards has been shown to bring an advantage in terms of efficiency of pollination, as certain wild bee species (e.g. Megachilidae; *Osmia*) outperform managed pollinators in specific contexts (Sedivy & Dorn, 2014). Moreover, a pan-European study by Cahenzli

et al. (2019) found that managed interrows support alternative prey for natural enemies, ensuring their persistence even when pest populations are low. Additionally, the vegetation of the interrows serve as overwintering and refugee habitat for beneficial arthropods, offering shelter during the winter season (Judt et al., 2019) or intensive orchard management practices (Jonsson et al., 2008). While vegetation structure and plant species' traits likely influence arthropod communities in these semi-natural habitats, their precise effects remain insufficiently understood. Further research is needed to determine how interrow selection and management can optimize vegetation structure to support beneficial arthropods. Moreover, although considerable attention has been given to pollinators and natural enemies (Fountain, 2022), other functional groups, such as alternative prey or organisms performing other fundamental ecological functions, have been neglected (but see Lundin et al., 2023).

Hay meadows and grasslands were once among the most widespread semi-natural habitats in the European agricultural landscape (Gustavsson et al., 2011). Through centuries of pastoralism or mowing activities, they were established on cleared woodland, shrublands, or drained marshland (Hejman et al., 2013). The management regime, particularly mowing and slight fertilisation, is crucial for maintaining these habitats. Controlled disturbance helps regulate competitive species, allowing rarer and more specialised species to thrive (Herzon et al., 2021; Lanta et al., 2009). Low-input, extensive meadows management has create among the most important and species-rich semi-natural habitats in Europe (Lepš, 1999). Due to their high diversity in plant species, these meadows support a wide range of arthropods, fostering complex ecological interactions (Welti et al., 2017). In particular, the richness and abundance of entomophilous plant species attracts many pollinators, thereby sustaining intricate pollination networks (Ebeling et al., 2008).

Changes in traditional management practices significantly impact plant species composition, habitat structure, and the associated arthropod community (Simons et al., 2014). Both intensification and abandonment lead to distinct ecological shifts with different consequences for plant and animal communities. On one hand, more intensive agricultural practices, such as ploughing, considerable fertilisation and frequent, intensive mowing, result in the impoverishment of the plant community (Uchida & Ushimaru, 2014), and particularly of entomophilous species. Overall, management intensification favours species adapted to high nutrient availability and frequent biomass removal, reducing overall plant diversity and changing plant community structure (Lepš, 1999). On the other hand, when management is abandoned, the meadow gradually undergoes natural succession, with shrubs and trees progressively encroaching. Over time, tall grasses and woody plants gradually increase in abundance, gradually replacing the specialised herbaceous species typical of traditional meadows (Petermann & Buzhdygan, 2021).

Besides habitat attributes, effectiveness of ecological intensification practices is expected to also depend on the landscape context in which they are implemented (Grab et al., 2018; Tschardt et al., 2005); that is, the effectiveness of restoration actions depends on both local and landscape constraints. The spatial configuration of landscapes (e.g., size, shape, and arrangement of patches with different use or cover), along with landscape composition, defined as the proportion of different land use/land cover types, is increasingly recognized as a crucial factor influencing biodiversity and the provision of associated ecosystem services in agricultural

systems (Gilby et al., 2018; Martin et al., 2019). In line with landscape ecology theory, a well-structured landscape enhances habitat connectivity, facilitates species movement, and promotes ecological interactions (Fahrig, 2013), ultimately supporting key ecosystem functions such as pollination and pest control.

However, previous studies have reported conflicting findings regarding the effects of increased landscape complexity (Martin et al., 2019). For example, many ecological processes exhibit nonlinear relationships between the intensity of an intervention and the resulting provision of ecosystem services. (Lindborg et al., 2017) hypothesized that certain population-based ecosystem services, such as crop pollination and biological control (Bengtsson 2010; Kremen et al., 2007; Tschardt et al., 2007), may only be effectively sustained when management interventions exceed a critical threshold. This suggests that small or incremental changes may have limited impact, whereas reaching a specific level of intervention is necessary to trigger significant ecological benefits (Tambosi et al., 2014). The intermediate landscape-complexity hypothesis, proposed by Tschardt et al. (2012), suggests that local conservation management is most effective in moderately simple agricultural landscapes, specifically those where natural or semi-natural habitats do not exceed 20% of the area. Accordingly, it is crucial to strategically plan interventions to maximise their benefits for biodiversity and ecosystem services (J. M. Holland et al., 2017). This emphasises the importance of carefully planning and implementing restoration projects to establish semi-natural habitats effectively and integrate them into the surrounding landscape (Gilby et al., 2018). Understanding how landscape composition and configuration interact, along with the relationship between local and landscape-scale features, is therefore essential for developing sustainable agricultural strategies that enhance productivity while conserving biodiversity.

Thesis structure

This thesis is structured into four main chapters, each addressing different aspects of semi-natural habitat management and restoration and their effects on plant and arthropod communities in agricultural landscapes. The first chapter examines the vegetation structure and plant functional traits within the inter-rows of an apple orchard and their influence on arthropod functional groups.

The second chapter explores the role of field edge management in soft wheat fields (*Triticum aestivum* L.), assessing its impact on predator and parasitoid communities, spillover effects at different distances into the crop fields, and pest control effects on winter wheat aphid communities.

The third chapter investigates how landscape composition and the extent of restored areas in agricultural intensive landscapes shape butterfly and bumblebee communities at local and landscape scales.

Finally, the fourth chapter analyses how management practices and climatic variables affect pollinator communities in hay meadows under different management intensities.

Together, these studies provide insights into the ecological dynamics of semi-natural habitats and their potential for enhancing biodiversity and ecosystem services in agricultural systems.

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Chapter 2

Ecological intensification: multifunctional flower strips support beneficial arthropods in an organic apple orchard

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Ecological intensification: multifunctional flower strips support beneficial arthropods in an organic apple orchard. *Plant Ecology* 225:499–509

Abstract

Flower strips are a fundamental part of agri-environment schemes in the Common Agricultural Policy (CAP). Although vegetation is central for many arthropod groups, a few studies have evaluated the effects of flower strip structural and functional attributes on arthropod communities. In this study, we explored the relationship between flower strip attributes and the abundance of different arthropod functional groups in annual flower strips located in an organic apple orchard. We surveyed plant and arthropod communities in 30 1 m × 6 m plots. In each plot, we collected data on species composition and vegetation structure (e.g., total cover, density, number of floral displays). For each plant species, we also retrieved data on leaf palatability and nutritional value. Arthropods were collected using sweep netting technique. Structural and functional attributes of the flower strip revealed a crucial role in regulating arthropod abundance, which however depended on the specific arthropod functional group. We identified three main attributes (plant species richness, plant species composition, vegetation density) of flower strips that should be considered when implementing multifunctional flower strips. Specifically, plant species richness to ensure complementarity of resources and niches, plant species composition to ensure complementary floral resources and vegetation density to ensure sheltering microhabitats and suitable microclimatic conditions and to increase the density of floral resources. Our results suggest that by considering structural and functional attributes of flower strips, it is possible to design multifunctional flower strips with greater effectiveness as measures for ecological intensification.

Keywords: Agri-environmental measures; Agroecosystem; Arthropod functional groups; Flower strip structure; Multifunctionality; Plant traits

Introduction

Over the past few years, ecological intensification has emerged as a nature-based approach to support agricultural production while reducing harmful environmental impacts (Garibaldi et al., 2019). The main assumption of ecological intensification is that by managing specific components of biodiversity, it is possible to enhance agricultural productivity by either complementing or replacing high-input management practices, with the ultimate goal of reducing environmental impacts and associated costs without limiting crop production (Kleijn et al., 2019).

The presence of seminatural habitats such as hedgerows and perennial seminatural grasslands in agroecosystems has been shown to be effective in sustaining communities of beneficial arthropods and preserving associated ecosystem services (Tscharntke et al., 2021). Seminatural habitats are created and maintained for their ability to provide feeding resources as well as shelter, overwintering, and nesting sites to beneficial arthropods, which are generally rarefied in intensive agricultural systems (Geiger et al., 2009; Landis, 2017). Additionally, the effectiveness of agri-environmental measures, such as flower strips, is influenced by the extent of seminatural habitats on the landscape context, serving as reservoirs and source population for beneficial arthropods (Eeraerts, 2023).

Among the most widely implemented agri-environmental measures are flower strips, a fundamental part of agri-environment schemes in the Common Agricultural Policy (CAP). Flower strips are usually established to improve pollination service and have been shown to actually increase the richness and abundance of pollinators, especially bees and hoverflies (e.g., A. J. Campbell et al., 2017, Ganser et al., 2021, Lowe et al., 2021). Flower strips can also support biological control, positively influencing parasitoids and predators by supplying nectar and pollen for adults, serving as overwintering refugia or providing an additional prey source for larvae (Ganser et al., 2019; J. M. Holland et al., 2016; Wäckers & Van Rijn, 2012). However, the effect of flower strips on beneficial arthropods depends on several factors related to both flower strip attributes (e.g., plant species composition, plant community structural and functional attributes (e.g., leaf area, leaf toughness and palatability, leaf C and N content)) and the target arthropods. For example, Von KönigsLöw et al. (2022) reported a different effect of the same flower strip on hoverflies and bees in an apple orchard. Hence, despite the large body of research on the effect of flower strips on beneficial arthropods, there are still many doubts on how to design and manage flower strips to promote multifunctionality, i.e., the ability of flower strips to simultaneously support a diverse arthropod community thereby assuring the supply of different ecosystem services (e.g., Albrecht et al., 2020, Bommarco et al., 2013).

Although vegetation is central for many animal species groups including arthropods (J. M. Holland et al., 2016; Kotze et al., 2022), it is often disregarded in studies on flower strips focusing on fauna (Schmidt et al., 2020). For example, small-scale variation in plant community cover and height has been shown to provide greater diversity of resources, shelter and nesting sites (Woodcock et al., 2007) and support a higher arthropod diversity compared to more structurally simplified plant communities (Mata et al., 2021; Threlfall et al., 2017). Plant species composition also has a major impact on the arthropod community, as different floral morphologies have different levels of accessibility and different arthropod taxa may have different mouthparts

and abilities to deal with different floral morphologies (e.g., Araj & Wratten, 2015, Branquart & Hemptinne, 2000). In addition, while perennial grasses support predators by providing relatively stable refugia during the cold season, the richness and abundance of entomophilous forbs may be crucial for both parasitoids and pollinators, as they provide floral resources such as nectar and pollen that enhance their survival and fecundity (Bianchi & Wäckers, 2008; Fantinato et al., 2021).

The predominant focus of studies on functional traits has centred on those associated with arthropod communities (Greenop et al., 2023), yet the studies on plant functional attributes are still limited within agroecosystems (Perović et al., 2018) even though they are expected to play a crucial role in influencing the composition of arthropod communities. Plant functional traits associated with plant resource use, growth, and life history strategies (e.g., leaf area, leaf toughness and palatability, leaf C and N content) are often studied to explore plant-environment and plant-plant interactions (e.g., Blumenthal et al., 2020, Fantinato et al., 2023); however, being also related to leaf nutritional value (e.g., C:N ratio; Pérez-Harguindeguy et al., 2013) and resistance to herbivory (e.g., leaf toughness; Pérez-Harguindeguy et al., 2013), these traits can help explain the richness and abundance of herbivorous (Storkey et al., 2013) and saprophagous arthropods (Ganault et al., 2022). Similarly, the classification of arthropods into functional groups has the potential to disentangle the complex relationships between arthropods and their functions within ecosystems (Balzan et al., 2014).

Considering the potential contribution of flower strips to the supply of multiple ecosystem services, the aim of this study was to uncover structural and functional attributes of flower strips that can guide flower strip design to maximise their role in the maintenance of different functional groups of beneficial arthropods in the agricultural systems. We hypothesise that structural and functional attributes of the flower strip differently affect arthropod community composition and the abundance of different functional groups of arthropods. We expect that structural and functional attributes of the flower strip play a different role in regulating arthropod abundance depending on the specific functional group considered. For example, the quantity of floral resources conceivably is a crucial factor in targeting pollinator and parasitoid functional groups, while this same attribute is likely to have no influence on e.g., herbivores that are supposed to be affected by functional attributes related to leaf nutrient content or leaf toughness.

Materials and methods

Study site

The study was conducted at a 2.7 ha organic apple orchard (45°24'28.872"N 11°9'34.416" E) in Caldiero (Verona, north-eastern Italy). The orchard is organic certified and conforms to all EU and Italian regulations ruling the production of organic crops, including EU Regulation 2018/848/EU and LN 9.03.2022, n. 23.

The soil composition of the orchard is clay-loam. The mean annual temperature is 14.3 °C with a mean high temperature of 31.3 °C in July and a low of -1.1 °C in January. The average annual rainfall is 756.3 mm, peaking in May and November and lowering in January and March.

The apple trees in the orchard are organized in regular rows, each of them 2 m apart. Each apple tree has branches arranged along the row and are spaced 3 m apart. The main apple cultivar grown in the orchard is "Gala" and M9 is used as rootstock. To control *Cydia pomonella* (L.) presence and damage on apple fruits,

pheromone disruption was applied. Typical fungicide treatments were applied as needed during the period between April and June to control Powdery mildew and Apple scab damages. All treatments were performed with chemical products allowed by organic certification.

In the apple orchard, flower strips were sown every second intermediate interrow, while spontaneous herbaceous vegetation was left in the other interrows (Figure 1). The seed mix used for the flower strips was a commercial seed mix consisting of a total of 19 plant species (2 grasses and 17 forbs), including both annual and biennial species whose main purpose was to attract pollinator insects (Table S2). The flower strips were sown in March and tillage was done in May of the same year for green manure purposes. Before and during sowing, the soil was worked using a ripper and a rotary harrow with a seeder.

Data collection

On the first week of May 2022, we established 30 1 m × 6 m sampling plots within the interrows of the apple orchard sown with the seed mix. We sampled plant and arthropod communities inside each 1 m x 6 m sampling plots previews placed on two consecutive days in the second week of May 2022, which corresponded to the peak of biomass production of the flower strip. To avoid edge effects, each plot was placed 6 m from the nearest end of the interrow. Each plot was further divided into six smaller sub-plots of 1 m × 1 m (Figure 1).

For each 1 m × 1 m sub-plot, we recorded structural attributes of the plant community: percentage cover of vascular plants (%), plant height measured with a rigid ruler at the centre of the sub-plot (cm) and canopy closure (%). Canopy closure was estimated by measuring the Leaf Area Index (LAI) using a convex model of a spherical crown densiometer. Canopy closure provides an estimate of the complexity of canopy stratification and the light quantity that reaches the ground; that is, the highest values of canopy closure correspond to monostratified canopies that intercept most of the light (Jennings, 1999; Liira et al., 2002).

In addition, during the sampling of structural attributes of the plant community, at the level of the whole sampling plot (1 m x 6 m) we recorded and identified to the species level each vascular plant species and their cover (%) and the total number of floral displays of entomophilous plant species as an indicator of the quantity of available floral resources. Depending on the plant species, a floral display consisted of a single flower (e.g., *Linum usitatissimum* L.), a flowering head (e.g., *Trifolium incarnatum* L. inflorescence) or a group of flowers appearing together in a recognizable visual unit (e.g., *Vicia villosa* Roth).

We collected the arthropod community using a sweeping net with 10 sweeping shots per sampling plot (1 m × 6 m), on sunny days with no or little wind. Sampling was conducted the next day after the sampling of the vegetation, twice per day, from 10 a.m. to 1 p.m. (morning) and from 1 p.m. to 4 p.m. (afternoon), to ensure the collection of arthropods that exhibit different daily periods of activity (Fantinato et al., 2018). To avoid damage to the plant community, we used 40 cm diameter entomological net instead of a classic sweeping net (Burgio et al., 2016). After collection, the arthropods were placed in plastic bags and taken to the laboratory for identification (Table S1). The collected arthropods were classified at the lowest possible taxonomic level. Each taxonomic group was then assigned to a functional group based on expert knowledge and literature sources. Identified arthropod functional groups included the following trophic groups: chewing herbivores, sap-sucking herbivores, pollen and nectar feeders, parasitoids, predators, aquatic saprophages and terrestrial

saprophages (Goulet and Huber 1993; Marshall 2012; Marshall 2018). In addition, we also included the category of pollinator due to their important ecological service.

In case arthropods belonged to different functional groups at different stages of their life cycle, we considered only the trophic condition of larvae since usually it is the longest stage in their lifecycle. Thus, regarding e.g., Argidae that are chewing herbivores as larvae, and pollen and nectar feeders as adults, we considered them as chewing herbivore. When a taxon included species of different trophic levels, we considered the dominant category. For example, since most of Chalcidoidea families are parasitoids, all collected Chalcidoidea were included in this group, although Chalcidoidea also includes Agaonidae with herbivore larvae. We considered as pollinator all taxa corresponding to bees and non-bee pollinators according to recent literature (e.g., Ollerton,

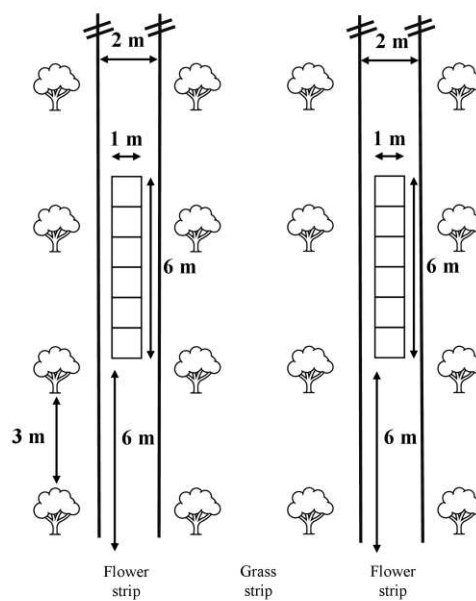


Figure 1: Planting size and positioning of the sampling plots within the apple orchard interrows

2017, Requier et al., 2023) where no data were available, we included in this group the taxa where adults regularly visit flowers as flower visitors and with dimensions higher than 3 mm (e.g., Rader et al., 2011). If arthropods belonged to the functional group of pollinators in addition to their trophic group, we counted them in both functional groups (i.e., the sum of individuals included in the functional groups is higher than the total number of individuals recorded). Individuals of Aphididae and Formicidae were not counted because the collection technique we used (i.e., sweeping net) is not suitable for quantifying their abundance (Dewar et al., 1982; Zina et al., 2022).

Plant functional traits

To investigate the relationship between functional traits of plants and functional groups of arthropods, we selected and extracted three plant traits from the global database TRY 3.0 (Kattge et al., 2020) that are related to plant size, leaf toughness or palatability, and nutrient content. We selected Leaf Area (LA) (mm²), Leaf dry matter content (LDMC) (g/g), and Leaf nitrogen content per dry mass (LNC) (mg/g) (Mooney & Gulmon, 1982; Pérez-Harguindeguy et al., 2013; Storkey et al., 2013). All trait data were checked, and we excluded

data related to studies in which plant individuals were grown under controlled environmental conditions. For each 1 m x 6 m sampled plot, the community weighted mean (CWM; equation 1) of each selected plant trait was calculated as the average trait value in the community weighted by species abundance (Garnier et al., 2004):

$$\text{CWM (trait } x) = \sum_{i=1}^n p_i x_i \text{ (equation 1)}$$

where CWM (trait x) is the CWM for a x trait, p_i is the relative cover of species i in the community and x_i is the trait value for the species i .

Data analysis

To investigate the relationship between the structural and functional attributes of flower strips and the abundance of individual arthropods of each functional group (i.e., chewing herbivores, parasitoids, pollinators, predators, and terrestrial saprophages) we performed GLMMs (package lme4). For each arthropod functional group, we included the abundance of individuals as dependent variable and the total cover of vascular plants (%), plant height (cm), canopy closure, plant species richness, total number of floral displays of entomophilous plants, and CMWs of functional traits (CMW_{LA}, CMW_{LDMC}, CMW_{LNC}) as independent variables. The total cover of vascular plants (%), plant height (cm) and canopy closure were calculated at plot level by averaging the values recorded in the six 1 m x 1 m sub-plots. Since the arthropod samples collected in the morning and afternoon were treated as replicates, plot identity was included in the model as random factor. Negative binomial distribution (function glmer.nb, log as link function) was chosen for all arthropod functional groups as data were overdispersed (dispersion test function; package AER; O'Hara and Kotze 2010).

For each GLMM, we followed the independent variable selection procedure for the mixed effects models (Zuur et al., 2010). At the beginning of the selection procedure, we included all the independent variables. We checked for possible collinearity between the independent variables using Spearman's rank correlations and retained those variables that were not highly correlated with each other (i.e., Spearman's $r < 0.7$). Since plant height (cm) and canopy closure were collinear ($r > 0.7$), we decided to include in the model only the canopy closure, because canopy closure provides a comprehensive picture of the complexity of canopy stratification, which also contains the information conveyed by the mean vegetation height. Using a stepwise backward selection, we eliminated the non-significant variables from the model at each step until only terms with $P < 0.05$ remained in the model. The analysis was performed for each functional group of arthropods, with the exception of sap-sucking herbivores and aquatic saprophages. As the Aphidoidea were not counted, the results for the group of sap-sucking arthropods would have been incomplete and unreliable, as Aphidoidea are also sap-suckers. As for the group of aquatic saprophages, these organisms, which spend most of their trophic life under water, are not necessarily associated with the presence of terrestrial flower strips. All analyses were performed using R version 4.2.2 (R Core Team 2019).

Results

Overall, 32 plant species were recorded in the sampling plots (Table S2). Forbs dominated over grasses both in number (27 vs. 5, respectively) and in mean coverage per plot ($75.5 \pm 10.19\%$ vs. $21.8 \pm 10.76\%$, respectively). Although commercial plant species accounted for only 44% of the total plant species pool recorded, they contributed an average of $92.46 \pm 5.85\%$ (mean $\pm$ SD) to the total cover of vascular plants, while spontaneous plant species contributed only $6.84 \pm 0.72\%$. The most abundant plant species were *Vicia villosa* ($25.50 \pm 18.06\%$), *Secale cereale* L. ($16.47 \pm 12.46\%$) and *Taraxacum officinale* (Weber) ex Wiggers ($13.59 \pm 23.00\%$).

Although sown with the same seed mix, the structural and functional attributes of the flower strips differed (Table 1; Table S3), with canopy closure and the number of floral displays the most variable attributes.

Table 1 Flower strip attributes. For each attribute, the mean and standard deviation are reported.

Flower strip attributes	Mean $\pm$ SD
Total cover of vascular plants (%)	97.29 ± 3.29
Plant height (cm)	60.33 ± 17.57
Canopy closure	7.17 ± 8.02
Plant species richness	14.60 ± 1.92
Number of floral displays	304.27 ± 192.71
CWM _{LA} (mm ²)	2574.06 ± 681.08
CWM _{LDMC} (g/g)	0.15 ± 0.01
CWM _{LNC} (mg/g)	47.04 ± 3.18

Regarding the arthropod community, we collected a total of 3,952 individuals belonging to 9 orders (i.e., Araneae, Coleoptera, Dermaptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Orthoptera) (Table S1). Herbivores were the most abundant functional group (46.32%, of which 40.66% were chewing herbivores and 5.66% were sap-sucking herbivores), followed by saprophages (31.36%; of which 27.64% were terrestrial and 3.72% aquatic) and parasitoids (14.07%). The less abundant functional groups were pollinators (4.69%) and predators (3.55%). At the plot level, the abundance of individuals belonging to different functional groups was found to vary greatly between the flower strips (Table 2).

Table 2 Summary statistics for the recorded functional groups of arthropods. For each functional group, the minimum and maximum range, the mean and standard deviation and the total number of individuals recorded in the flower strips based on individual samples are reported.

Arthropod functional group	Number of individuals		
	Min - Max	Mean $\pm$ SD	Total individuals
Chewing herbivores	7 - 95	27.88 $\pm$ 18.76	1673
Sap-sucking herbivores	0 - 19	3.88 $\pm$ 3.17	233
Parasitoids	1- 20	9.65 $\pm$ 4.88	578
Pollinators	0 - 14	3.22 $\pm$ 2.91	194
Predators	0 - 12	2.43 $\pm$ 2.42	146
Aquatic saprophages	0 - 9	2.55 $\pm$ 2.05	153
Terrestrial saprophages	1 - 103	18.95 $\pm$ 17.76	1138

Different arthropod functional groups responded differently to different structural and functional attributes of flower strips (Table 3). The abundance of chewing herbivores showed a significant positive relationship with plant species richness and CWM_{LNC} , while their abundance decreased at increasing CWM_{LDMC} (Table 3; Figure 2a-2b-2c). The abundance of parasitoids showed a significant positive relationship with total vegetation cover (%) and canopy closure (Figure 2d-2e) and a significant negative relationship with the number of floral displays (Table 3; Figure 2f). The abundance of pollinators showed a significant positive relationship with both total cover of vascular plants (%) and number of visual displays (Table 3; Figure 2g-2h). The abundance of terrestrial saprophages significantly decreased in abundance at increasing CWM_{LDMC} and number of floral displays; while their abundance increased at increasing CWM_{LNC} (Table 3; Figure 2i-2j-2k). The abundance of predators did not show any significant relationship with structural and functional attributes of flower strips. Finally, CWM_{LA} showed no significant relationship with the abundance of any arthropod group.

Table 3 Statistics of the relationships between the abundance of arthropod functional groups and structural and functional attributes of flower strips. Only statistically significant results are reported.

Dependent variable	Independent variable	Estimated coefficient	SE	z-score	<i>P</i>	χ^2
Chewing herbivore abundance	Plant species richness	0.109	0.038	2.831	0.011	6.492
Chewing herbivore abundance	CWM _{LDMC}	-22.744	7.657	-2.970	0.007	7.248
Chewing herbivore abundance	CWM _{LNC}	0.0733	0.020	3.555	0.001	9.676
Parasitoid abundance	Total cover of vascular plants	0.083	0.032	2.603	0.011	6.415
Parasitoid abundance	Canopy closure	0.041	0.012	3.225	0.001	10.467
Parasitoid abundance	Number of floral displays	-0.001	0.000	-3.502	<0.001	11.037
Pollinator abundance	Total cover of vascular plants	0.209	0.056	3.748	<0.001	13.429
Pollinator abundance	Number of floral displays	0.165	0.000	3.256	0.001	10.043
Terrestrial saprophage abundance	Number of floral displays	-0.001	0.000	-2.413	0.016	5.606
Terrestrial saprophage abundance	CWM _{LDMC}	-33.820	10.116	-3.031	0.002	8.138
Terrestrial saprophage abundance	CWM _{LNC}	0.101	0.028	3.580	0.000	10.531

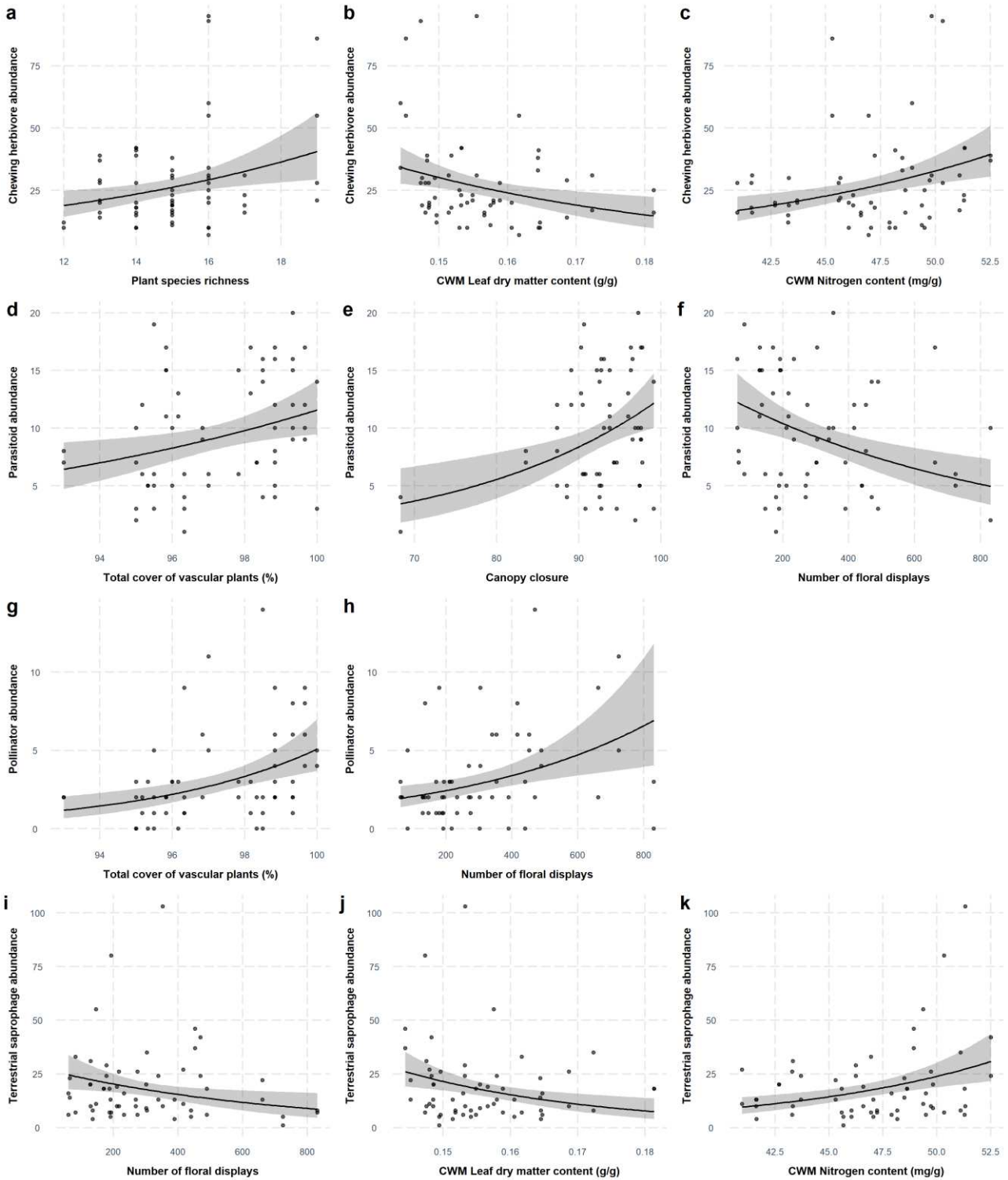


Figure 2: Relationship between vegetation structure variables (Total cover of vascular plants (%), Number of floral displays, Canopy closure, Plant species richness) and community weighted mean of plant functional traits (CWM_{LDMC}, CWM_{LNC}) of arthropods functional groups (chewing herbivores, parasitoid, pollinator, saprophage). Lines represent the estimates of the Generalised Mixed Linear Models (GLMMs). Black points are original data points, while the grey band represents 95% confidence interval around the regression line. Only significant results are shown in the figure.

Discussion

In the present study we have shown that flower strips can support a diversified set of functional groups of arthropods thereby proving the potential to be a multifunctional landscape element in agroecosystems. The results showed that the abundance of arthropods belonging to different functional groups is influenced by structural and functional attributes of the strips. Interestingly, however, the role played by the attributes of the flower strips on the abundance of arthropods changed depending on the functional group considered. Namely, while the abundance of chewing herbivores and terrestrial saprophages was more related to the functional attributes of the flower strip, i.e., the toughness/palatability of the leaves, and nutritional value of the plant species, the abundance of parasitoids and pollinators was more related to the structural attributes of the plant community, such as the total cover of vascular plants, the canopy closure and the number of floral displays.

As expected, the abundance of pollinators increased with the number of floral displays. This result confirms previous studies that found that flower abundance and associated availability of pollen and nectar favours a richer and more abundant pollinator community (e.g., Bartholomée et al., 2020, Feltham et al., 2015), highlighting the crucial role of flower strips in increasing pollination capacity (Feltham et al., 2015; Korpela et al., 2013) and crop pollination of adjacent fields (Albrecht et al., 2020). However, pollinator abundance was also positively correlated to the total cover of vascular plants, i.e., to vegetation density; thus, not only the number of floral displays but also greater plant species cover contributed to greater pollinator abundance. As flower strips are usually dominated by entomophilous forbs, higher vascular plant cover leads to dense flower patches that are more attractive to pollinators because they allow them to reduce travel time among sparse patches and save energy (Elliott & Irwin, 2009; Schütz et al., 2022). In addition to the important cover and floral resources provided by flowering plants in seed mixtures, we also noted the significance of spontaneous plant species, particularly *Taraxacum officinale* L. As previously found by Eeraerts et al. (2021) spontaneous plant species normally present in apple orchard interrows can provide additional floral resources for pollinators in agricultural landscape.

A similar trend was observed for parasitoids, whose abundance increased with increasing cover of vascular plants and canopy closure of the flower strips, namely, with higher plant density. Parasitoids may prefer dense flower strips since they provide sheltering microhabitats as well as stable and suitable microclimatic conditions to complete their life cycle (Langellotto & Denno, 2004). Conversely, and contrary to what has been observed in previous studies (e.g., A. Campbell et al., 2017, Pollier et al., 2019), we found that parasitoid abundance was negatively related to the number of floral displays. Indeed, several studies have found that parasitoid richness and abundance are higher when associated with abundant floral resources (Dib et al., 2012; Jervis et al., 1993). However, as reported by Wäckers (2005), some plant species, such as *Vicia sepium* L., may be unattractive or even repulsive to foraging parasitoids. In addition, mouthpart features of most parasitoids (Wäckers, 2004) limit their feeding to exposed nectaries and generally to flowers with simple floral morphologies (Willmer et al., 2011). The negative relationship between parasitoid abundance and the number of floral displays observed in this study could therefore be due to the complexity of floral morphologies of the dominant plant species (i.e., *Vicia villosa*, *Vicia sativa* and *Lathyrus oleraceus* Lam.). This suggests that when

establishing flower strips to attract and maintain parasitoids, it is crucial not only to consider flower abundance and associated pollen and nectar availability but also carefully select plant species based on their floral morphologies.

As stated above, the abundance of chewing herbivores and terrestrial saprophages was more related to the functional attributes of the flower strip. Chewing herbivores represented the most abundant functional group with abundance increasing in flower strips with higher plant species richness, lower CWM_{LDMC} , and higher CWM_{LNC} . While the relationship with leaf palatability and nutritional value was somehow expected, the relationship with plant species richness highlights an interesting issue. The increase in herbivore abundance at increasing plant species richness suggests that the presence of different plant species can provide resources for herbivores with different feeding preferences (species-specific relationships); that is, a greater variety of resources supports a greater diversity of consumers. This result is certainly fascinating from a biodiversity perspective but must be treated with caution from an agronomic perspective, as undesirable pest species can also benefit from the food sources. On the other hand, species-rich flower strips can also serve as a sink for herbivorous arthropods, which tend to feed within the strip rather than on crops. In addition, the abundance of generalist herbivores can also provide alternative prey sources for pests, leading to increased control of agricultural pests. Therefore, only ‘appropriate diversity helps’ (Gurr et al., 2005), and the creation of flower strips requires careful assessment of structural and functional attributes to meet the needs of beneficial arthropods without promoting pest species (Winkler et al., 2003).

Terrestrial saprophages showed a trend similar to that of chewing herbivores with a negative relationship with CWM_{LDMC} and a positive relationship with CWM_{LNC} . Terrestrial saprophages play an important role in the functioning of terrestrial ecosystems being key regulators of plant litter decomposition. The relationship between terrestrial saprophage abundance and nitrogen content and palatability of plant biomass has been mostly described considering the litter layer (e.g., David & Gillon, 2009, Purse et al., 2012), and litter nitrogen content has been shown to strongly influence the abundance of terrestrial saprophages (Haddad et al., 2009; Moço et al., 2010). However, it has to be considered that defensive or supporting structures that increase leaf toughness and reduce palatability remain in plant tissue after plant death and thus influences the properties of litter biomass (Kazakou et al., 2009). We can thus assume that the relationships between terrestrial saprophages and litter are mediated by the functional composition of the strip, which thus becomes a crucial feature to be considered for the maintenance of this functional group of arthropods. The fact that the number of saprophages decreased with the number of floral displays was somewhat surprising and indicates a relationship that still needs to be explored and deserves further investigation. A possible explanation arises when we consider that most of the terrestrial saprophages collected in the present study belong to taxa that feed on pollen and nectar as adults and usually visit flowers with open nectaries. The Drosophilidae, for example, which were the most abundant among the terrestrial saprophages, are generally unable to manipulate flowers with complex morphology and, in temperate regions, are more likely to visit species from the Apiaceae or Asteraceae family (Larson et al., 2001), which were underrepresented in the species pool of the flower strips. Thus, also in this

case, species composition in terms of floral morphology and nectar accessibility, becomes a crucial attribute to consider when designing a flower strip.

Finally, we could not find any relationship between the structural and functional attributes of the flower strips and the abundance of predators. Predators depend upon stable environmental conditions and their establishment requires more time compared to other functional groups of arthropods (e.g., pollinators; Hussain et al., 2021). Tschardt et al. (2016) suggest that agri-environmental measures may not effectively support biocontrol agents due to various reasons. The flower strips in the study site are often disturbed by farming practices, such as grass cutting and transit of agricultural vehicles for work practices on apple trees. These practices may limit habitat suitability for predators, creating a continuous disturbance (Thorbek & Bilde, 2004). Experimental data on the provision of ecosystem services and especially on multifunctionality are still rare (Schütz et al., 2022). Although our study only provides a temporal snapshot of conditions during the peak of the growing season of annual flower strips, we can outline some attributes of flower strips that should be taken into account to increase the effectiveness in ecological intensification and to implement multifunctional flower strips:

- 1) plant species richness: since species richness and functional richness are inherently linked, creating flower strips with higher plant species richness can help maximise resource and niche complementarity, enhancing their ability to support more wide and diverse arthropod communities. It is important to note that richer flower strips may attract higher numbers of herbivorous arthropods, which could potentially become pests of associated crops;
- 2) plant species composition: the selection of plant species is crucial in promoting floral resources that can support different beneficial arthropod groups that have different resource needs and feeding habitats. Careful consideration should be given to the choice of plant species in the seed mix in relation to the beneficial arthropod groups and the ecological function of the floral strips that we wish to enhance. Particular attention should be paid to the floral morphology of flowering plant species, as not all morphologies are suitable for beneficial arthropod groups that do not have specialized mouthparts, such as parasitoids;
- 3) vegetation density: the management of flower strips can be crucial in creating and maintaining an optimal vegetation structure. This, in turn, creates different ecological niches for various beneficial arthropod groups. Agricultural practices have a significant impact on these groups, which require a stable, stratified, and closed habitat to inhabit. Therefore, it is important to manage them to avoid excessive disturbance during the early stages of vegetative development, thus creating a stratified and dense vegetation of the flower strips. The age of the flower strip deserves a final remark. Annual flower strips are certainly appealing to farmers who can adapt their location to crop rotation; however, due to frequent farming practices they are subjected to, annual flower strips fail in assuring suitable overwintering and nesting opportunities for many arthropod groups, including predators. Conversely, if properly managed, perennial structures are likely to offer more stable habitats thereby effectively contributing to promote local arthropod population growth over time.

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Supplementary materials

Table S1: Orders, lower taxonomic groups, and number of individuals (abundance) for each arthropod functional groups recorded.

Functional groups	Orders	Lower taxonomic group	N. of individuals
Chewing herbivore	Coleoptera	Elateridae	1
Chewing herbivore/Pollinator	Diptera	Tephritidae	1
Chewing herbivore	Orthoptera	Acrididae	2
Chewing herbivore	Orthoptera	Tettigoniidae	2
Chewing herbivore/Pollinator	Hymenoptera	Argidae	2
Chewing herbivore	Coleoptera	Chrysomelidae	3
Chewing herbivore/Pollinator	Lepidoptera	Geometroidea	4
Chewing herbivore/Pollinator	Coleoptera	Cetoniinae	5
Chewing herbivore/Pollinator	Lepidoptera	Gelechioidea	5
Chewing herbivore	Hymenoptera	Cynipoidea	15
Chewing herbivore	Diptera	Opomyzidae	20
Chewing herbivore	Diptera	Cecidomyiidae	40
Chewing herbivore/Pollinator	Diptera	Anthomyiidae	111
Chewing herbivore	Diptera	Agromyzidae	183
Chewing herbivore	Coleoptera	Curculionoidea	218
Chewing herbivore	Diptera	Chloropidae	1061
Sap-sucking herbivores	Hemiptera	Lygaeidae	1
Sap-sucking herbivores	Hemiptera	Pentatomidae	16
Sap-sucking herbivores	Hemiptera	Cicadellidae	81
Sap-sucking herbivores	Hemiptera	Miridae	135
Parasitoid	Hymenoptera	Evanioidea	1
Parasitoid	Hymenoptera	Ceraphronidae	4
Parasitoid/Pollinator	Diptera	Tachinidae	4
Parasitoid	Hymenoptera	Diaprioidea	22
Parasitoid	Hymenoptera	Platyastroidea	31
Parasitoid	Hymenoptera	Chalcidoidea	180
Parasitoid	Hymenoptera	Ichneumonoidea	336
Pollen feeders/Pollinator	Hymenoptera	Anthophila	31
Predator /Pollinator	Diptera	Syrphini	2
Predator	Hemiptera	Nabidae	2
Predator	Coleoptera	Staphylinidae	3
Predator	Diptera	Empidoidea	3
Predator	Areneae	Opiliones	4
Predator	Neuroptera	Chrysopidae	5
Predator	Hemiptera	Berytidae	7
Predator	Dermaptera	Forficulidae	8
Predator	Hemiptera	Anthocoridae	28
Predator	Araneae	Araneae	84
Acquatic saprophage/Pollinator	Diptera	Stratiomyidae	16
Acquatic saprophage	Diptera	Tipulomorpha	25
Acquatic saprophage	Diptera	Culicomorpha	112
Terrestrial saprophage	Diptera	Anthomyzidae	1

Functional groups	Orders	Lower taxonomic group	N. of individuals
Terrestrial saprophage	Diptera	Chyromyidae	1
Terrestrial saprophage	Diptera	Dryomyzidae	1
Terrestrial saprophage	Diptera	Asteiidae	2
Terrestrial saprophage	Diptera	Lonchopteridae	2
Terrestrial saprophage	Diptera	Ephydriidae	3
Terrestrial saprophage	Diptera	Scathophagidae	4
Terrestrial saprophage	Diptera	Sphaeroceridae	5
Terrestrial saprophage/Pollinator	Diptera	Muscidae	5
Terrestrial saprophage/Pollinator	Coleoptera	Melyridae	8
Terrestrial saprophage	Diptera	Phoridae	25
Terrestrial saprophage	Diptera	Scatopsidae	31
Terrestrial saprophage	Diptera	Lauxaniidae	40
Terrestrial saprophage	Diptera	Milichiidae	52
Terrestrial saprophage	Diptera	Sciaridae	120
Terrestrial saprophage	Diptera	Sepsidae	130
Terrestrial saprophage	Coleoptera	Nitidulidae	171
Terrestrial saprophage	Diptera	Drosophilidae	537

Table S2: Plant species and sources: Sp=spontaneous; SM=seed mix. *Seed mix composition of the is expressed as percentage of each species in the seed mixture as given by the seller (Na = spontaneous plant species). For each plant species the mean cover per plot (%) and standard deviation is also reported (Not recorded= species present in the seed mix but not recorded in the plots).*

Plant species	Family	Species source	Seed mix composition (%)	Mean species cover (%) $\pm$ SD
<i>Avena barbata</i> Pott ex Link	Poaceae	Sp	Na	0.17 $\pm$ 0.91
<i>Brassica napus</i> L.	Brassicaceae	SM	1.67	5.10 $\pm$ 4.89
<i>Calendula officinalis</i> L.	Asteraceae	SM	0.30	Not recorded
<i>Calepina irregularis</i> (Asso) Thell.	Brassicaceae	Sp	Na	0.23 $\pm$ 0.48
<i>Capsella bursa-pastoris</i> (L.) Medik.	Brassicaceae	Sp	Na	0.09 $\pm$ 0.22
<i>Cerastium glomeratum</i> Thuill.	Caryophyllaceae	Sp	Na	0.03 $\pm$ 0.10
<i>Convolvulus arvensis</i> L.	Convolvulaceae	Sp	Na	0.33 $\pm$ 1.27
<i>Coriandrum sativum</i> L.	Apiaceae	SM	0.31	0.28 $\pm$ 0.49
<i>Cota altissima</i> (L.) J.Gay	Asteraceae	SM	0.31	0.67 $\pm$ 3.65
<i>Eruca vesicaria</i> (L.) Cav.	Brassicaceae	SM	0.67	5.27 $\pm$ 6.18
<i>Fumaria officinalis</i> L.	Papaveraceae	Sp	Na	0.33 $\pm$ 0.18
<i>Fagopyrum esculentum</i> Moench	Polygonaceae	SM	3.34	Not recorded
<i>Geranium dissectum</i> L.	Geraniaceae	Sp	Na	0.23 $\pm$ 0.73
<i>Lamium purpureum</i> L.	Lamiaceae	Sp	Na	2.24 $\pm$ 3.47
<i>Lathyrus oleraceus</i> Lam.	Fabaceae	SM	16.68	8.33 $\pm$ 8.71
<i>Linum usitatissimum</i> L.	Linaceae	SM	1.67	3.19 $\pm$ 5.11
<i>Lolium multiflorum</i> Lam.	Poaceae	Sp	Na	3.67 $\pm$ 5.49
<i>Lupinus albus</i> L.	Fabaceae	SM	2.50	Not recorded
<i>Matricaria chamomilla</i> L.	Asteraceae	Sp	Na	0.43 $\pm$ 1.85
<i>Phacelia tanacetifolia</i> Benth.	Hydrophyllaceae	SM	5.00	9.13 $\pm$ 8.77
<i>Poa trivialis</i> L.	Poaceae	Sp	Na	2.55 $\pm$ 3.30
<i>Raphanus raphanistrum</i> L.	Brassicaceae	SM	1.67	8.00 $\pm$ 5.34
<i>Secale cereale</i> L.	Poaceae	Sp	Na	16.47 $\pm$ 12.46
<i>Senecio vulgaris</i> L.	Asteraceae	Sp	Na	2.81 $\pm$ 4.42
<i>Sinapis alba</i> L.	Brassicaceae	SM	3.34	4.18 $\pm$ 4.68
<i>Sonchus asper</i> (L.) Hill	Asteraceae	Sp	Na	0.09 $\pm$ 0.20
<i>Sonchus oleraceus</i> L.	Asteraceae	Sp	Na	1.88 $\pm$ 3.78
<i>Stellaria media</i> (L.) Vill.	Caryophyllaceae	Sp	Na	2.35 $\pm$ 3.54
<i>Taraxacum officinale</i> (L.) W.W.Weber ex F.H.Wigg.	Asteraceae	Sp	Na	13.59 $\pm$ 23.00
<i>Trifolium incarnatum</i> L.	Fabaceae	SM	1.67	7.60 $\pm$ 4.83
<i>Trifolium alexandrinum</i> L.	Fabaceae	SM	3.34	Not recorded
<i>Trifolium ochroleucon</i> Huds.	Fabaceae	Sp	Na	0.07 $\pm$ 0.37
<i>Triticum aestivum</i> L.	Poaceae	SM	13.34	11.00 $\pm$ 12.14
<i>Veronica persica</i> Poir.	Plantaginaceae	Sp	Na	1.68 $\pm$ 2.15
<i>Vicia faba</i> L.	Fabaceae	SM	13.34	Not recorded

Plant species	Family	Species source	Seed mix composition (%)	Mean species cover (%) $\pm$ SD
<i>Vicia sativa</i> L.	Fabaceae	SM	14.18	10.07 $\pm$ 18.30
<i>Vicia villosa</i> Roth	Fabaceae	SM	3.34	25.50 $\pm$ 18.06

Table S3: Flower strip attributes per plot. Plot identity, mean total vegetation cover (%), mean vegetation height (cm), mean LAI (Leaf Area Index) and standard deviation and total number of visual displays for each sampling plot (1 × 6 m).

Plot ID	Mean total vegetation cover (%) ± SD	Mean vegetation height (cm) ± SD	Mean LAI ± SD	Total number of visual displays
1	99.67 ± 0.82	56.83 ± 6.94	5.83 ± 3.3.7	417
2	98.83 ± 2.04	40.00 ± 7.07	12.00 ± 7.59	453
3	96.00 ± 3.52	40.83 ± 8.01	12.00 ± 7.38	217
4	99.33 ± 1.03	50.00 ± 11.83	10.33 ± 7.81	139
5	95.50 ± 4.64	41.67 ± 9.83	8.83 ± 8.77	93
6	98.17 ± 1.83	38.33 ± 10.80	9.17 ± 5.67	171
7	98.50 ± 1.97	43.33 ± 12.52	6.83 ± 5.71	193
8	96.17 ± 3.25	57.50 ± 6.89	3.67 ± 3.44	225
9	100.00 ± 0.00	80.00 ± 10.49	0.67 ± 0.82	492
10	99.33 ± 1.03	77.50 ± 11.73	3.17 ± 3.43	234
11	98.83 ± 2.04	40.00 ± 7.07	10.83 ± 6.01	270
12	98.50 ± 1.97	49.17 ± 10.21	7.00 ± 4.24	470
13	96.33 ± 2.88	34.17 ± 9.17	30.33 ± 22.17	180
14	99.67 ± 0.82	63.33 ± 5.16	2.17 ± 0.98	310
15	98.83 ± 2.04	50.00 ± 8.37	6.50 ± 3.08	62
16	97.00 ± 3.10	68.33 ± 12.52	7.00 ± 3.03	725
17	95.00 ± 3.16	65.00 ± 8.94	5.00 ± 4.05	390
18	95.33 ± 3.27	67.50 ± 6.89	2.33 ± 1.63	455
19	96.83 ± 2.14	77.50 ± 7.58	2.17 ± 2.40	345
20	95.17 ± 2.93	58.33 ± 8.76	9.00 ± 5.18	275
21	95.83 ± 3.76	66.67 ± 6.06	3.33 ± 2.73	131
22	95.83 ± 3.76	63.33 ± 6.83	5.83 ± 5.49	135
23	95.50 ± 3.39	69.17 ± 7.36	6.83 ± 2.04	189
24	98.83 ± 2.04	85.83 ± 3.76	2.00 ± 1.41	662
25	95.00 ± 3.16	98.50 ± 6.75	2.83 ± 1.60	831
26	98.33 ± 2.07	67.17 ± 6.65	5.33 ± 3.83	303
27	97.83 ± 2.48	70.00 ± 10.00	7.33 ± 7.94	194
28	93.00 ± 8.49	51.67 ± 8.76	15.67 ± 7.61	66
29	99.33 ± 1.03	79.17 ± 8.61	2.50 ± 1.64	354
30	96.33 ± 2.88	59.17 ± 8.61	8.67 ± 5.99	147

Chapter 3

Low-intensity field edge management enhances natural enemy diversity in winter wheat (*Triticum aestivum* L.) but does not improve aphid control

Abstract

European agricultural landscapes comprise a mosaic of cultivated fields and semi-natural habitats that play a fundamental role in supporting agricultural biodiversity and associated ecosystem services, particularly biological pest control. Among semi-natural habitats, field edges have been recognised as important refuges, and as trophic and overwintering habitats for pest natural enemies such as parasitoids and predators. However, the degree to which different field edge management practices affect the structure and effectiveness of natural enemy communities remains poorly understood. This study investigates the effect of field edge management in winter wheat fields on both vegetation and natural enemy attributes. It also evaluates the effectiveness of aphid pest control (Hemiptera: Aphididae: *Sitobion avenae* Fabricius). Fieldwork was conducted on organic farms in northeastern Italy, comparing two winter wheat fields under different edge management regimes: intensively managed (characterised by tillage and biannual mowing) and extensively managed (no-tillage and single annual mowing). Vegetation attributes were assessed within the edge habitat, and arthropod communities were sampled at increasing distances from the edges (0, 5, 10 and 40 m) into the fields. Aphid community sampling and the assessment of pest control effectiveness were performed at different distances from the edges (5, 10, 40 m). Statistical analysis revealed that extensively managed edges harboured higher taxonomic group richness of natural enemies up to 10 m from the edges. In contrast, aphid abundance and parasitism rates did not differ significantly between management types. These findings suggest that extensive field edge management can promote more diverse natural enemy communities and their spatial distribution within fields. Enhancing vegetation heterogeneity and floral resource availability through extensive edge management may thus promote beneficial arthropods in agroecosystems.

Keywords: Field edge management, Agroecology, Biological pest control, Vegetation structure, Aphid parasitism, Winter wheat

Introduction

The European agricultural landscape is characterised by an intricate mosaic of cultivated areas and numerous semi-natural habitats (Marshall, 2004). These semi-natural areas, represented by more or less intensively managed non-productive agricultural areas, have been shrinking in recent decades (Jeanneret et al., 2021). These semi-natural areas have proven crucial for conserving agricultural biodiversity as they are the habitat for numerous animal and plant species in Europe (Billeter et al., 2008). Consequently, conserving these habitats has become a key objective in recent European policies to protect biodiversity in agricultural environments (J. M. Holland et al., 2017). Numerous studies have highlighted that semi-natural habitat play a fundamental role in conserving agricultural biodiversity and maintaining associated ecosystem services (e.g., García-Feced et al., 2015, Mkenda et al., 2019). Among these services, biological pest control is crucial for managing crop pests, limiting damage, and ensuring sustainable crop production (Price & Martinsen, 1994; Swinton et al., 2006).

Maintaining effective biological pest control requires understanding and conserving the natural enemies that regulate pest populations. Natural enemies (i.e., organisms that contribute significantly to controlling pest populations) comprise various taxa. In European agricultural landscapes, the primary groups are parasitoid arthropods and predators (Kleijn et al., 2019). Although both groups contribute to pest control, their modes of action and habitat requirements differ. Parasitoids are generally specialised and closely associated with particular host organisms (Strand & Obrycki, 1996), whereas predators tend to be more generalist in their feeding habits (Memmott et al., 2000). Several studies have shown that many parasitoids rely on alternative energy sources, such as nectar and honeydew, to sustain their activity (e.g., Gillespie et al., 2016, Lewis et al., 1998). In contrast, some predator groups, such as Coccinellidae, require additional trophic resources (Lundgren & Seagraves, 2011), while others depend on alternative prey, including arachnids (Östman, 2004). Effective management of semi-natural areas creates microhabitats and provides the trophic resources necessary for the life cycle of natural enemies (Landis et al., 2000). Specifically, semi-natural habitats such as managed field edges (i.e., narrow, linear areas along the perimeter of cultivated fields) are important for conserving natural enemy fauna in the agricultural landscapes (e.g., Marshall, 2004, Marshall & Moonen, 2002). Moreover, the abundance and richness of natural enemy communities are influenced by factors such as the availability of floral resources (e.g., pollen and nectar, Heimpel & Jervis, 2005) and the presence of alternative prey or hosts (Landis et al., 2000). The strategies promoted by conservational biological control focus on preserving and managing semi-natural habitats to favour the presence of the above-mentioned natural enemies (El-Wakeil et al., 2017). Therefore, knowing how the management of semi-natural habitats such as field borders can favour natural enemies is essential for controlling insect pests and their damage.

Triticum aestivum L. is one of Europe's major crops and holds significant global economic importance (Grote et al., 2021). This crop is vulnerable to various diseases and pest infestations, including aphids (Afzal et al., 2015). Aphid species such as *Sitobion avenae* Fabricius, *Rhopalosiphum padi* L., and *Metopolophium dirhodum* Walker frequently cause significant economic damage (Poehling et al., 2007). Pest control is typically achieved through chemical, biological, and cultural methods and integrated pest management

approaches (Barzman et al., 2015). Several studies have examined how conservation biological control strategies can enhance natural enemy populations near wheat fields. For instance, organic farming practices have been linked with improved local biological control compared to intensive management systems (Winqvist et al., 2012). However, while these practices support stronger biological control than conventional practices, the mechanisms linking soil management practices, such as tillage, to above-ground ecosystem services remain poorly understood (Rusch et al., 2013).

In contrast, intensive practices typical of conventional management can directly harm arthropod populations through mechanical damage and indirectly by degrading habitat quality and reducing the availability of alternative prey (e.g., J. M. Holland, 2004). Additionally, edge management of wheat fields influences natural enemy communities and their capacity to control aphids, though the effectiveness of these practices remains uncertain. For example, conservation tillage has been shown to favour predator communities and enhance predation and parasitism of wheat aphids (Tamburini et al., 2016), while other research indicates that management practices only partially affect natural enemy populations, resulting in inconsistent aphid control (Sacco–Martret De Prévile et al., 2022).

Several studies have examined how natural enemy abundance and pest control vary with distance from field edges; however, few have evaluated both aspects simultaneously with edge management. For instance, a study on tomato fields bordered by hedgerows found that natural enemy abundance decreased up to 200 meters from the edge, with varying spillover ranges for different organisms (Morandin et al., 2014). Similarly, tailored flower strips in potato fields have boosted natural enemy densities and enhanced pest suppression near field edges (Tschumi et al., 2016). While studies by Landis et al. (2000) and Bianchi et al. (2006) underscore the importance of habitat management for conserving natural enemies, the relation of management of field edges and the evaluations of both pest control efficacy and the community of natural enemies within fields is still overlooked.

Considering the potential of agricultural semi-natural habitat management in supporting natural enemy communities and the ecosystem service of pest control, the objective of this study is to evaluate the effect of management intensity on two different field edge managements on parasitoid and predator communities and their effect in controlling pests within wheat fields. We hypothesise that extensive management of soft wheat field edges may favour the composition and abundance of the natural enemy communities that inhabit them. We also expect this effect to influence the pest control process by favouring greater control over the aphid community, a common and damaging pest of soft wheat, through a reduction in their abundance and a greater number of pest aphids. In addition, we expect extensive management to favour the presence and diversity of natural enemies and a pest control effect at a greater distance from field borders towards the interior of winter wheat fields.

Materials and methods

Study site

The study was conducted on the organic farm "Ca' Bredo," located at 45° 16' 9.5196" (N) and 12° 6' 34.9056" (E) in Codevigo, Padova, in northeastern Italy (Figure S1). This farm primarily produces oilseed and protein

crops, with additional areas dedicated to vineyards for wine production. All crops are certified organic and comply with EU and Italian regulations ruling organic crop production, including EU Regulation 2018/848/EU and LN 9.03.2022, n. 23. Agronomical treatments within the farming area utilized only chemical products permitted under organic certification. The soil composition in the study area features a deep, moderately coarse-textured surface, transitioning to a coarse texture in the substrate. It is alkaline in reaction and highly calcareous, with the parent material consisting of calcareous sands (Gasparetto et al., 2005). Over the past five years, the average temperature has been 14.30 ± 7.48 °C, with August being the warmest month (average temperature of 23.96 ± 0.58 °C) and January the coldest (average temperature of 3.6 ± 1.58 °C). The average annual rainfall during this period was 721.36 ± 176.71 mm, with peaks in May and November and a low in February (ARPA, 2024). Within the farm, two square fields of winter wheat (*Triticum aestivum* L.) were selected. The edges of wheat fields were chosen based on their management practices. The edges were managed in one field with an extensive approach (no-tillage and edge cutting at the end of the growing season). In contrast, in the other field, the edges were managed with an intensive approach (surface tillage and edge cutting at the beginning and end of the growing season). For each field, two opposite edges were selected (Low intensity edges mean length: 108.60 ± 1.87 m, mean areas: 157.42 ± 5.06 m; high intensity edges mean length: 147.59 ± 2.72 m, mean areas: 219.31 ± 203.73 m) (Figure S1).

Data collection

In the last week of April 2022, one sampling plot measuring 1 m x 6 m was placed within each edge of the selected fields, resulting in four sampling plots (Figure 1). In each sampling plot, the plant community was sampled during the second half of May 2022, at the peak of vegetation biomass. Each vascular plant species was identified, and its percentage cover (%) was estimated. The identification of all entomophilous plant species in the sampling plots occurred during the second half of May 2022 and the first half of June 2022. The total number of floral displays was counted to indicate the availability of floral resources. A floral display can consist of a single flower (for example, *Linum usitatissimum* L.), a flowering head (such as the inflorescence of *Trifolium incarnatum* L.), or a group of flowers that appear together as a recognizable visual unit (e.g., *Vicia villosa* Roth). In addition, we recorded the structural characteristics of the plant community during the second half of May 2022 and the first half of June 2022. Each sampling plot was divided into six sub-plots measuring 1 m x 1 m. In each sub-plot, we recorded the percentage cover of vascular plants (%), measured plant height (in cm) using a rigid ruler at the centre of the sub-plot, and estimated canopy closure (%). Canopy closure was evaluated by measuring the Leaf Area Index (LAI) with a convex model of a spherical crown densiometer. This measurement estimates the complexity of canopy stratification and the amount of light reaching the ground; higher values of canopy closure correspond to monostратified canopies that intercept most of the available light (Jennings et al. 1999; Liira et al. 2002). Beside field edge sampling plots, three belt transects were established within the fields at three different distances from the edge (5 m, 10 m, and 40 m) in the last week of April 2022 (Figure 1). Each belt transect included four 1 m x 1 m sampling plots spaced 5 m apart. In each sampling plot, aphid presence was assessed by observing the leaves on the *Triticum aestivum* L. plants during the second half of May 2022 and the first half of June 2022. Aphids were identified by species, and the

number of individuals was counted. Additionally, aphid mummies were counted in each sampling plot to estimate the ecosystem service of pest control. Arthropod communities were collected using the sweep net technique after sampling the vegetation and aphids in edge sampling plots (1 m x 6 m) and field sampling plots (1 m x 1 m). The arthropod community in each edge sampling plot was sampled using 12 sweeping shots, while in each field sampling plot, three sweeping shots were used for a total of 12 across the entire transect. All samplings took place on sunny days with little or no wind. Sampling was conducted the day following the vegetation and aphid sampling, occurring twice daily: once from 10 a.m. to 1 p.m. (morning) and again from 1 p.m. to 4 p.m. (afternoon) to capture arthropods active at different times. To mitigate damage to the plant community, a 40 cm diameter entomological net was used instead of a traditional sweeping net (Burgio et al., 2016). After collecting, arthropods were placed in plastic bags and transported to the laboratory for identification. The collected arthropods were classified at least to the family level. Identified arthropods related to natural enemies of pest arthropods were included in the following trophic groups: parasitoids and predators (Goulet and Huber 1993; Marshall 2012; Marshall 2018). For arthropods that belong to different trophic groups at various life cycle stages, only the trophic condition of the larvae was considered, as this stage typically lasts the longest. For instance, individuals of the family Syrphidae were identified at the species level to determine the feeding habits of the larvae and assess their potential contribution to the predator trophic group. It is important to note that individuals of families Aphididae and Formicidae were not counted, as the collection technique (i.e., sweep net) was unsuitable for accurately quantifying their abundance (Dewar et al. 1982; Zina et al. 2022).

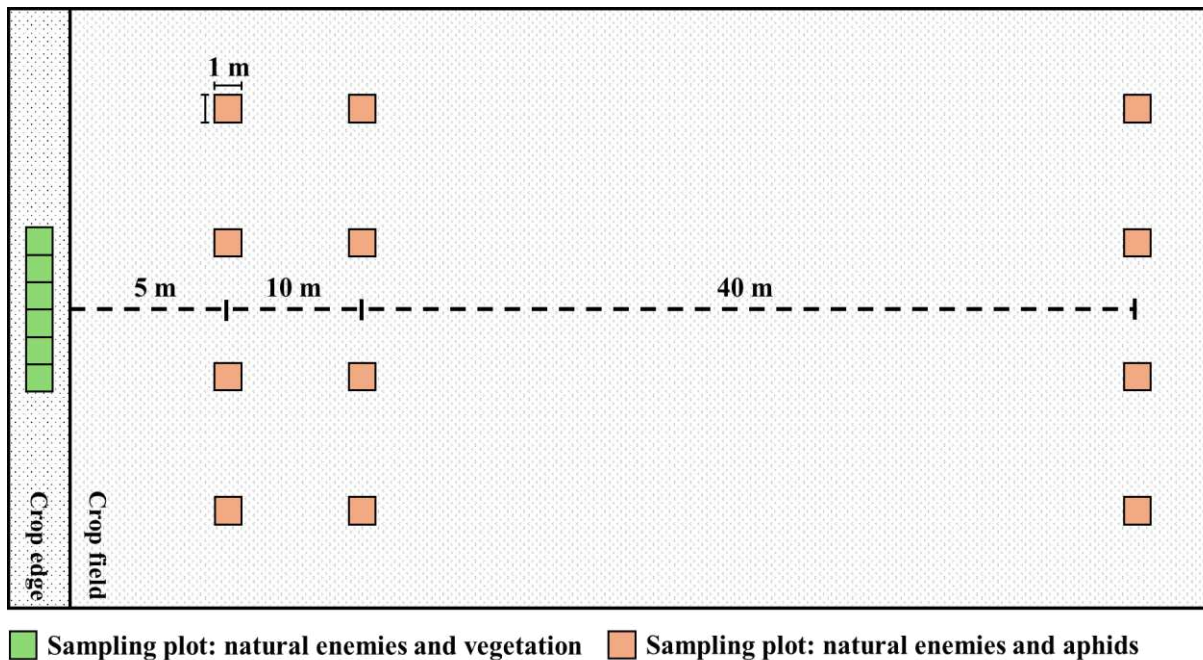


Figure 1: Vegetation, natural enemies and aphids sampling design.

Data analysis

Differences in natural enemy community attributes (i.e., taxonomic group richness and abundance of parasitoid and predator), aphid community attribute, and the effect of pest control (i.e. aphid abundance, aphid mummy abundance and aphid mummy percentage) between extensive and intensive management of edge systems were

analysed using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). PERMANOVA was selected because it tests the responses to one or more variables in relation to one or more factors (i.e. management type) using permutation methods on distance measures similar to ANOVA.

The Bray–Curtis dissimilarity index was chosen for this analysis because it considers differences in species abundance while ignoring joint absences, making it particularly suitable for ecological data. The analysis was conducted for each distance considered (0, 5, 10 and 40 meters for the enemy community attributes; 5, 10 and 40 meters for the aphid attributes) by performing seven separate PERMANOVA analyses. Analyses were performed using the 'adonis' function from the 'vegan' package in R (Oksanen et al., 2007). If the PERMANOVA analysis indicated significant differences between the types of edge management and the attributes of the natural enemy communities, a paired Wilcoxon signed-rank test using the 'Wilcox.test' function in R was conducted to identify significant differences between means. All analyses were performed in R version 4.2.2 (R Development Core Team 2022).

Results

From the vegetation sampling, a total of 25 plant species were recorded. In the extensive edges 23 plant species were recorded, while the high management type edges plant species recorded were 13. In the extensive edges, the plant species with the highest coverage were *Vicia sativa* L. ($25.5 \pm 34.6\%$), followed by *Alopecurus myosuroides* Huds. ($22.5 \pm 10.6\%$) and *Equisetum arvense* L. ($16.5 \pm 12.0\%$). In contrast, the intensive edges showcased *Avena barbata* Pott ex Link ($37.5 \pm 53.0\%$) as the dominant species, followed by *Solidago canadensis* L. ($15.0 \pm 21.2\%$) and *Matricaria chamomilla* L. ($8.5 \pm 9.2\%$) (Table S1).

The analysis of vegetation attributes revealed distinct structural characteristics between extensive and intensive edges (Table 1). Specifically, extensive edges exhibited higher average values for percentage vegetation cover and canopy closure than intensive edges. Furthermore, the sampling of entomophilous plant species identified 13 species in extensive edges and 6 species in intensive edges. Interestingly, the average number of floral displays was higher in intensive edges. *Matricaria chamomilla* L. had the highest number of floral displays in both edge types: 40.5 ± 47.02 in extensive edges and 174.00 ± 172.08 in intensive edges. *Papaver rhoeas* L. (19.25 ± 19.62) and *Convolvulus arvensis* L. (15.50 ± 14.53) were the second species higher in number of floral displays respectively in extensive and intensive edges.

Table 1: Vegetation attributes measured at extensive and intensive field edges. Values represent mean and standard deviation for percentage cover of vascular plants (%), vegetation height (cm), canopy closure (%), and number of floral displays.

Vegetation attributes	Extensive edges	Intensive edges
Percentage cover of vascular plants (%)	85.08 ± 13.21	69.96 ± 24.21
Vegetation height (cm)	53.71 ± 15.07	55.17 ± 40.16
Canopy closure (%)	87.05 ± 8.31	71.53 ± 20.80
Number of floral displays	26.61 ± 29.53	56.27 ± 108.71

During the two sampling periods, a total of 2001 arthropod was recorded. Specifically, intensive edges showed a total of 760 arthropods while extensive edges a total abundance of 1241 arthropods (Table S2). The sampling of the natural enemy community revealed variations in the attributes of different trophic groups between the two edge types (Table 2). For parasitoids, intensive edges contained 13 families, whereas extensive edges included 15 families. For the predator trophic groups, intensive edges included 11 families compared to 12 of extensive edges (Table S2). Among parasitoids, the most abundant taxonomic group in intensive edges were Scelionidae (53), Braconidae (49), and Pteromalidae (33). In extensive edges, Pteromalidae was the most abundant group (125), followed by Braconidae (124) and Scelionidae (75). Among predator taxonomic groups, intensive edges had Araneae (322) as the most abundant group, followed by Coccinellidae (40) and Hybotidae (38). Similarly, in extensive edges, Araneae (389) was the most abundant predator group, followed by Hybotidae (146) and Coccinellidae (49).

Table 2: Natural enemy attributes measured at extensive and intensive field edge systems. Values represent mean and standard deviation for taxonomic group richness and abundance of parasitoids and predators.

Natural enemy attributes	Extensive edges	Intensive edges
Taxonomic group richness of parasitoids	4.56 ± 2.02	2.47 ± 1.16
Taxonomic group richness of predators	3.66 ± 1.49	3.41 ± 1.39
Abundance of parasitoids	14.19 ± 15.82	5.56 ± 3.90
Abundance of predators	20.69 ± 13.35	14.47 ± 10.89

Sampling for aphids in the wheat fields identified only one species, *Sitobion avenae* Fabricius. In terms of abundance, intensive fields had on average 10.69 ± 11.74 (mean ± SD) aphids per plot, while extensive fields had 6.08 ± 7.95 aphids per plot. For the abundance of mummies, intensive fields had a mean of 1.15 ± 1.21 , compared to 0.44 ± 0.98 in extensive field margins. Patterns regarding aphid abundance, aphid mummy abundance and aphid mummy percentage (%) varied with distance from the edges, depending on the management type (Table 3).

Table 3: Aphid abundance, aphid mummy abundance and aphid mummy percentage (%) at different distances from extensive and intensive field edges (i.e. EE: extensive edges, IE: intensive edges). Values represent mean and standard deviation for aphid and aphid mummy abundance at 5, 10, and 40 meters from the field edge.

Distance from the edge (m)	Aphid abundance		Aphid mummy abundance		Aphid mummy percentage	
	EE	IE	EE	IE	EE	IE
5	4.69 ± 5.19	10.19 ± 11.99	0.50 ± 1.19	1.13 ± 1.29	12.89 ± 32.76	20.64 ± 33.49
10	7.31 ± 10.65	9.44 ± 9.52	0.38 ± 0.61	1.31 ± 1.43	15.24 ± 24.31	14.99 ± 33.13
40	6.25 ± 7.05	12.44 ± 13.52	0.44 ± 1.08	1.00 ± 0.88	9.82 ± 23.84	12.71 ± 26.65

PERMANOVA analyses revealed significant differences in the attributes of the natural enemy community based on management type (extensive versus intensive) (Table 4; Figure 2). The statistical analysis showed significant results for distances of 0 m, 5 m, and 10 m, but not for 40 m. Post-hoc analyses at 0 m distance indicated significant difference of taxonomic group richness of parasitoids, with extensive edges exhibiting greater values than intensive edges (Table 4; Figure 2a). At 5 m distance from the edges, Post-hoc analyses indicated significant difference of taxonomic group richness of predator with extensive edges exhibiting greater values than intensive edges (Table 4; Figure 2b). At 10 m distance from the edges, Post-hoc analyses indicated significant difference of taxonomic group richness of parasitoids with extensive edges exhibiting greater values than intensive edges (Table 4; Figure 2c). However, the analyses of aphid abundance, aphid mummy abundance and aphid mummy percentage between extensive and intensive edges showed no significant differences.

Table 4: Statistical analysis of the effect of management type of the field edges (extensive versus intensive) on parasitoids and predators attributes (i.e. taxonomic group richness of parasitoid, taxonomic group richness of predator, parasitoid abundance and predator abundance) at different distances from the edges (0, 5, 10 and 40 m). The table presents degrees of freedom (df), sum of squares total (SST), coefficient of determination (R^2), F-statistic (F), p-values, and significance levels from PERMANOVA tests. Additionally, Wilcox post-hoc test results are presented. Only statistically significant results are reported.

Distance 0 m						
Categorical variable	df	SST	R ²	F	<i>p-value</i>	Sign. Value
Management type	1	0.39393	0.18765	3.234	0.011	*
Wilcox post-hoc test						
Categorical variable	Dependent variable			<i>p-value</i>	Sign. Value	
Management type	Taxonomic group richness of parasitoids			0.01671	*	
Distance 5 m						
Categorical variable	df	SST	R ²	F	<i>p-value</i>	Sign. Value
Management type	1	0.18902	0.1747	2.9635	0.05	*
Wilcox post-hoc test						
Categorical variable	Dependent variable			<i>p-value</i>	Sign. Value	
Management type	Taxonomic group richness of predators			0.001206	**	
Distance 10 m						
Categorical variable	df	SST	R ²	F	<i>p-value</i>	Sign. Value
Management type	1	0.26018	0.24858	4.6313	0.018	*
Wilcox post-hoc test						
Categorical variable	Dependent variable			<i>p-value</i>	Sign. Value	
Management type	Taxonomic group richness of parasitoids			0.004817	**	

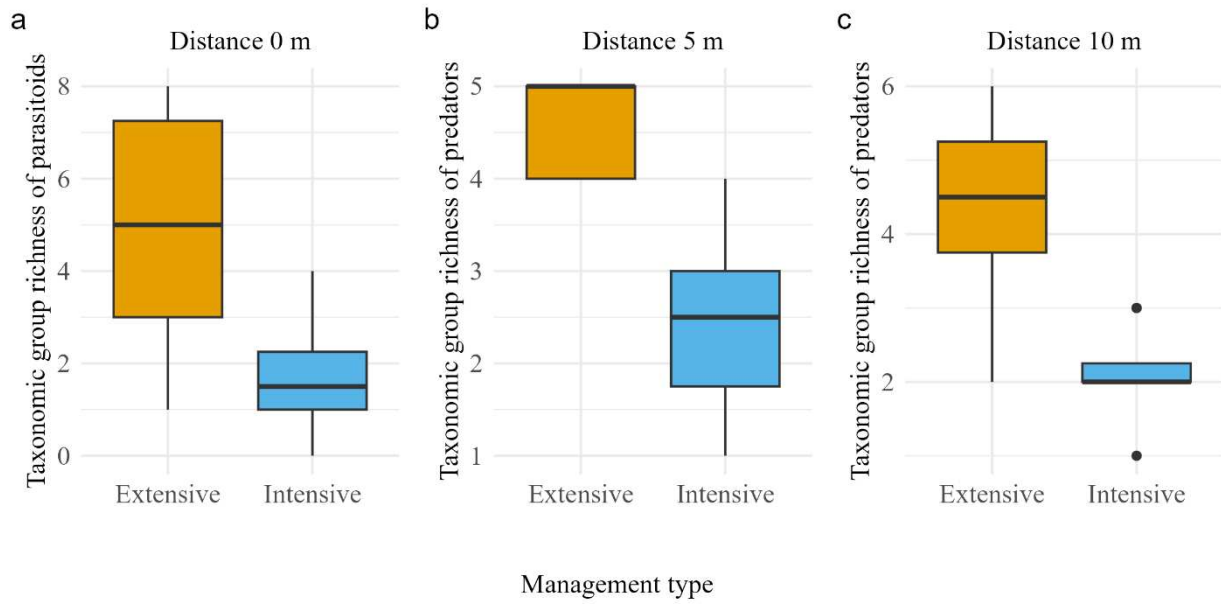


Figure 2: Taxonomic group richness of parasitoids and predators under different management types (extensive versus intensive) at different distances from the edges (0, 5, and 10 m). Only statistically significant results are reported.

Discussion

This study has shown that management intensity of field edges significantly influences vegetation and natural enemy communities. The way field edges are managed alters vegetation characteristics, such as cover, height, and species composition, that are crucial for providing trophic resources, shelter, and microhabitats to arthropods (J. Wang et al., 2023). For instance, total vascular plant cover and canopy closure promote heterogeneous microhabitats that facilitate spatial partitioning among parasitoids and predators (Favarin et al., 2024). Moreover, different plant traits can affect arthropod groups according to their specific resource and microhabitat requirements (Inagaki et al., 2022). Additional factors, including alternative trophic resources and prey, are essential for attracting and maintaining natural enemy populations in semi-natural habitats. (Knop et al., 2006) showed that arthropod diversity is often linked to plant species diversity and edge management, although responses may vary among groups.

Our results revealed that low-intensity field edge management supports the greater taxonomic richness of parasitoids and predators compared to high-intensity practices. This finding aligns with previous studies showing that extensive management practices, such as maintaining floral abundance and reducing chemical inputs, enhance natural enemy diversity (e.g., Gómez-Cabezas et al., 2022, Hassan et al., 2016). However, we did not observe a significant increase in natural enemy abundance under low-intensity management. One possible explanation is that both management types provide sufficient resources to sustain healthy populations within the most common taxonomic groups. For example, even though floral resources in high-intensity edges are less diverse, they may still support generalist parasitoids and predators through intermittent nectar availability or alternative prey (Crowther et al., 2023). In contrast, low-intensity edges may foster niche complementarity without necessarily boosting total abundance (Staab & Schuldt, 2020).

Our study further indicates that the most abundant parasitoid groups (Braconidae, Pteromalidae, and Scelionidae) and predator groups (including Arachnida, Hybotidae, and Coccinellidae) occur in both types of field edges. This suggests that predator and parasitoid groups with greater dietary versatility or mobility can adapt more readily to changes in edge management, thus maintaining stable populations in the agricultural landscape (Macfadyen & Muller, 2013). Generalist predators, such as arachnids, benefit from high habitat and dietary plasticity, enabling them to exploit resources in various environments (Saqib et al., 2022). Similarly, parasitoids capable of using multiple hosts or alternative resources like nectar and pollen thrive in both intensively and less intensively managed areas (Gillespie et al., 2016). These adaptive traits are likely to help them withstand disturbances caused by management practices.

Notably, parasitoid diversity was significantly higher in low-intensity edges at the field border (0 m) and up to 10 m into the field. In comparison, predator diversity peaked at 5 m from the edge. These spatial patterns likely reflect the two groups' resource requirements and mobility differences. The higher parasitoid diversity in low-intensity edges may result from the vegetation providing essential trophic resources (e.g., nectar, pollen, honeydew) and alternative hosts, which support diverse parasitoid assemblages (Bignal & McCracken, 1996). The observed association between parasitoid diversity and edge vegetation aligns with their ecological specialisation, given that many parasitoids depend on floral resources for sustenance and host availability for

reproduction (Lewis et al., 1998). The greater taxonomic diversity within 10 m of low-intensity edges also suggests a spillover effect, where parasitoids move into adjacent croplands to exploit host populations, in line with studies on parasitoid foraging behaviour (Cronin & Reeve, 2005).

In contrast, predators exhibited distinct spatial and ecological responses. Their broader dietary plasticity allows them to exploit various prey within crops, making them less dependent on edge-specific resources. Generalist predators, such as arachnids, tend to congregate near field edges and inside croplands, driven primarily by prey availability rather than microhabitat fidelity (Wimp et al., 2019). Nevertheless, low-intensity edges still supported greater predator taxonomic diversity than high-intensity systems, suggesting that less intensive management fosters niche diversification for these generalists. These findings underscore the importance of considering taxonomic identity when developing edge management strategies to enhance natural enemy diversity and pest control services (Perović et al., 2018; Wimp et al., 2019).

Agricultural practices that enhance vegetation structure and composition while minimising disturbance can improve natural enemy communities and foster resilient biocontrol services within crop fields (Tooker et al., 2020). Despite the observed differences in natural enemy diversity, our study did not find a significant effect of edge management on aphid abundance or parasitisation, as assessed through both mummy counts and mummy percentage.

This suggests that pest control services may depend more on the abundance of natural enemies than on their diversity (Mei et al., 2024). However, it is important to acknowledge that our evaluation focused exclusively on mummy abundance, capturing only aphid parasitism while not accounting for predation by predator groups. As a result, our view of the overall pest control service may be biased, given that the contributions of predators remain unassessed. Moreover, evaluations based solely on mummy counts indicate that the direct impact of natural enemies on pest control might be limited (Macfadyen et al., 2015). Nevertheless, a greater diversity of natural enemies could enhance pest control at the community level by simultaneously targeting multiple pest species (E. W. Evans, 2016). This highlights the need for future studies to assess pest control services across various pests and natural enemy groups.

Our study shows that low-intensity field edge management promotes the diversity of natural enemies within a limited spatial range. However, it is necessary to consider the limitations of our study. Indeed, the sampling was conducted over a single sampling season and considered a relatively small number of fields and field edges. For this reason, our findings should be interpreted cautiously, as they may not fully capture the temporal variability or broader applicability of these management effects. Specifically, we could not observe the long-term dynamics of predator and parasitoid communities or the dynamics of effectiveness in pest control on winter wheat aphids that could have requested more sampling seasons. Notwithstanding these limitations, extensive management of field borders shows the ability to contribute to conserving the agricultural biodiversity of natural enemy taxa. Further studies are needed to investigate the effect of field edge management on the conservation of agricultural biodiversity and the effect on the effectiveness of pest control offered by these semi-natural habitats.

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Supplementary materials

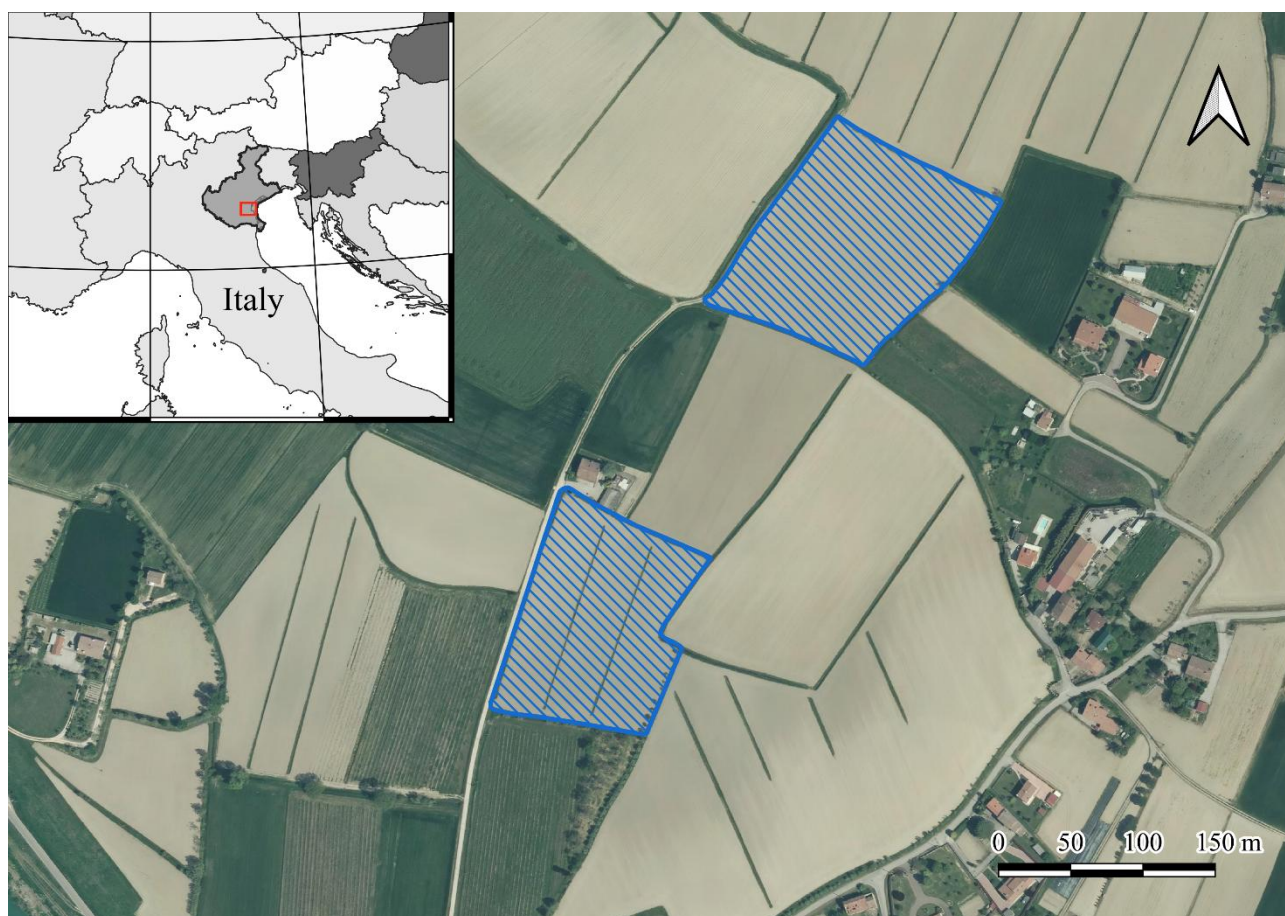


Figure S1: Study region and selected sampled fields. The farm under study is highlighted in red (top panel). Blue rectangles identify sampled fields.

Table S1: Mean and deviation standard of the percentage coverage (%) of the plant species detected in the field edges. Plant species nomenclature follows Bartolucci et al. (2024).

Plant species	Percentage cover (%)
<i>Alopecurus myosuroides</i>	12.03 ± 13.61
<i>Avena barbata</i>	20.75 ± 36.36
<i>Carex hirta</i>	1.25 ± 2.50
<i>Centaurea cyanus</i>	1.25 ± 2.50
<i>Convolvulus arvensis</i>	7.13 ± 8.78
<i>Cynodon dactylon</i>	5.00 ± 10.00
<i>Equisetum arvense</i>	8.75 ± 11.35
<i>Leucanthemum vulgare</i>	2.00 ± 4.00
<i>Lythrum salicaria</i>	0.50 ± 1.00
<i>Matricaria chamomilla</i>	6.00 ± 6.68
<i>Medicago lupulina</i>	2.25 ± 3.30
<i>Papaver rhoeas</i>	8.25 ± 4.72
<i>Phragmites australis</i>	3.75 ± 7.50
<i>Poa trivialis</i>	1.38 ± 2.43
<i>Polygonum aviculare</i>	0.25 ± 0.50
<i>Ranunculus repens</i>	0.25 ± 0.50
<i>Rubus occidentalis</i>	4.50 ± 5.26
<i>Rumex longifolius</i>	2.00 ± 4.00
<i>Solidago canadensis</i>	8.00 ± 14.70
<i>Taraxacum officinale</i>	1.38 ± 2.43
<i>Tragopogon pratensis</i>	0.50 ± 1.00
<i>Trifolium pratense</i>	3.75 ± 4.79
<i>Triticum aestivum</i>	1.13 ± 1.93
<i>Veronica persica</i>	0.58 ± 0.96
<i>Vicia sativa</i>	16.50 ± 23.36

Table S2: Order, lowest taxonomic group, abundance and type of natural enemy of the arthropods sampled in the edge systems.

Order	Taxonomic group	Abundance	Natural enemies
Araneae	Araneae	711	Predator
Coleoptera	Cantharidae	20	Predator
Coleoptera	Cetoniidae	5	-
Coleoptera	Chrysomelidae	6	-
Coleoptera	Coccinellidae	89	Predator
Coleoptera	Oedemeridae	12	-
Coleoptera	Staphylinidae	2	Predator
Diptera	Anthomyiidae	28	-
Diptera	Hybotidae	184	Predator
Diptera	Stratiomyidae	6	-
Diptera	Syrphidae	36	Predator
Diptera	Tachinidae	34	Parassitoid
Hymenoptera	Andrenidae	1	-
Hymenoptera	Aphelinidae	5	Parassitoid
Hymenoptera	Apidae	3	-
Hymenoptera	Braconidae	173	Parassitoid
Hymenoptera	Ceraphronidae	42	Parassitoid
Hymenoptera	Colletidae	1	-
Hymenoptera	Crabronidae	5	Predator
Hymenoptera	Cynipidae	2	-
Hymenoptera	Diapriidae	4	Parassitoid
Hymenoptera	Encyrtidae	3	Parassitoid
Hymenoptera	Eulophidae	13	Parassitoid
Hymenoptera	Eupelmidae	11	Parassitoid
Hymenoptera	Eurytomidae	2	Parassitoid
Hymenoptera	Halictidae	32	-
Hymenoptera	Ichneumonidae	23	Parassitoid
Hymenoptera	Megachilidae	1	-
Hymenoptera	Megaspilidae	5	Parassitoid
Hymenoptera	Mymaridae	14	Parassitoid
Hymenoptera	Platygastridae	14	Parassitoid
Hymenoptera	Proctotrupidae	1	Parassitoid
Hymenoptera	Pteromalidae	158	Parassitoid
Hymenoptera	Scelionidae	128	Parassitoid

Order	Taxonomic group	Abundance	Natural enemies
Hymenoptera	Torymidae	2	Parassitoid
Neuroptera	Chrysopidae	10	Predator
Rhynchota	Anthocoridae	9	Predator
Rhynchota	Microphysidae	2	Predator
Rhynchota	Nabidae	55	Predator
Rhynchota	Oxycarenidae	1	-
Rhynchota	Pentatomidae	106	-
Rhynchota	Reduviidae	2	Predator

Chapter 4

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

Sebastiano Favarin, Edy Fantinato, Andrea Della Bella, Gabriella Buffa. Butterflies as indicators of restoration success: Insights from habitat restoration in agricultural landscapes. (Submitted to Restoration Ecology)

Abstract

Ecological intensification through habitat restoration is increasingly recognised as an effective strategy to mitigate biodiversity loss and support pollinator populations. Pollinators, particularly butterflies (Lepidoptera: Papilionoidea and Hesperioidea) and bumblebees (Hymenoptera: Apidae: *Bombus* spp.), are critical to the functioning of ecosystems and serve as valuable indicators of environmental health. However, both groups are experiencing significant declines, making population monitoring essential for assessing the success of habitat restoration efforts. This study evaluated the impact of habitat restoration on butterfly and bumblebee communities in northern Italy, comparing restored and unrestored agricultural areas. Nine farms were selected where habitat restoration focused on the creation of pollinator-friendly habitats, including species-rich grasslands and flower strips. Monitoring was conducted along transects divided into sub-transects, passing through both restored and unrestored areas. The composition of land cover and land use at local and landscape scales were assessed using high-resolution land cover maps. Monthly surveys were conducted before and after restoration measures (2022–2023) from May to September, focusing on species richness and abundance. Butterflies and bumblebees were classified into specialist and generalist species based on their life history traits. The results showed that habitat restoration had a positive effect on butterfly richness and abundance, especially in areas with greater landscape heterogeneity. Generalist butterfly species benefited more than specialists, possibly due to the remaining species pool in a landscape heavily shaped by urban sprawl and agricultural intensification. In contrast, bumblebees reacted less sensitively to restoration measures. A spillover effect was observed, where butterfly richness and abundance increased in neighbouring unrestored areas, suggesting that habitat restoration can improve the wider landscape. Our results emphasise the potential of butterfly species as bioindicators for monitoring the success of habitat restoration and provide insights for improving ecological intensification strategies in agricultural landscapes.

Keywords: Ecological intensification, habitat restoration, landscape heterogeneity, life-history traits, pollinators, spillover.

Introduction

In recent decades, there has been a growing global emphasis on the need to shift agricultural practices towards 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 (Bommarco et al. 2013; 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 semi-natural 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 emphasise landscape-scale restoration, including the re-establishment and proper management of high quality semi-natural 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).

Overall, habitat restoration has been shown to increase species richness and abundance of key pollinator groups (e.g., Cariveau et al. 2020; 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 acting at different levels of organisation and scale (Faichnie et al. 2021; Scheper et al. 2013; Woodcock et al. 2021).

Arguably, pollinator life history traits such as resource requirements, mobility and specialisation 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 behaviour, i.e., that are able to exploit the floral resources of a wide range of plant species, and exhibit high mobility, are expected to colonise newly established or improved semi-natural 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 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 colonise 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 restoration effectiveness in enhancing pollinator richness and abundance in neighbouring, unrestored areas has been less studied (Scheper et al. 2015; Jönsson 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 the spillover effect 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 semi-natural 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 spillover effects. 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 specialisation 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 responses to the restoration of semi-natural 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 neighbouring, unrestored areas, indicating possible spillover effects? 3. How do differences in landscape composition influence the effectiveness of local habitat restoration in enhancing pollinator richness and abundance?

Materials and methods

Study site

The study was conducted on nine farms in the eastern Po Valley in Italy (see Fig. S1), a region heavily shaped by urban sprawl and intensive agricultural practices (Lorenzato et al. 2024). 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 semi-natural habitats. Strategic planning was informed by previous studies indicating that the most effective approach combines large habitat patches, which support the persistence of pollinator populations, with smaller, spatially dispersed patches that ensure a continuous distribution of floral resources across the landscape (Boetzi et al. 2021; Torchio et al. 2024). 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 interrows and along field margins (Favarin et al. 2024). In line with the objectives of the CAP 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 hectares and flower strips with an average area of around 1,500 square metres.

Restoration methods followed established best practices in ecological restoration (Török et al. 2011) and nature-based solutions, combining the sowing of locally sourced seed mixtures with the planting of native herbaceous seedlings. 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. To further support the restoration process, native plug plants were introduced to accelerate habitat establishment and ensure early floral resource availability. In selecting species for both seed mixtures and plug plants, care was taken to maximise the diversity of floral traits (shape, size, colour, resources) while taking into account habitat-specific ecological requirements, local climate and projected climate change impacts, prioritising 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 behaviour, 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.

Data collection

Data collection focused on butterflies (Lepidoptera: Papilionoidea and Hesperioidea) and bumblebees (Hymenoptera: Apidae: *Bombus* spp.), as these groups are widely recognised as key pollinator indicators in monitoring programmes (e.g., Potts et al. 2024) due to their ease of field identification and the extensive knowledge on their ecology and behaviour (Amiet et. 1996; Paolucci 2010). Moreover, increasing attention is being directed towards these two pollinator groups due to their significant declines in recent decades (Vray et al. 2019; Habel et al. 2019), and their potential to be used in monitoring schemes (e.g., Potts et al. 2024).

A single sampling transect was established on each of the nine farms, ranging in length from 700 to 1,000 metres. Transect placement was designed with the aim of quantifying direct variations in butterfly and bumblebee communities across restored and unrestored areas. Each sampling transect was divided into 100-

metre sub-transects, which were then categorised as either restored ($\geq 75\%$ of the sub-transect length traversing restored area; $n = 157$) or unrestored ($< 75\%$ of the sub-transect length traversing unrestored area; $n = 192$). The landscape context along each 100 metres sub-transect was assessed using a high-resolution land cover map based on aerial photographs provided by the Veneto Region (resolution: $0.2 \text{ m} \times 0.2 \text{ m}$) in QGIS 3.28.15. Considering that different scales can highlight 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 metres buffer (local scale) and 600 metres buffer (landscape scale). In each sub-transect and for each buffer, all landscape elements identifiable at a scale of 1:500 were drawn and categorised 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”) prior to the calculation of their percent cover in each map. Ditches, drains and banks characterised 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 (e.g., artificial water drainage channels, rivers and lakes) have been mapped and quantified, however they were excluded from further analyses due to the overall low percentage of cover (Table S2). Standardised transect counts (Pollard & Yates 1993) were utilised 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, and all observed butterflies and bumblebees within a 5-meter range ahead and 2.5 metres on either side of the surveyor were counted. 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. Furthermore, the surveys were conducted in conditions of wind speed that did not exceed four on the Beaufort scale (Pollard & Yates 1993). Standardised transect counts were carried out in 2022, immediately after completion of the restoration activities (ex-ante situation), and again in 2023 (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 et al. 2020).

All recorded individuals were identified to the species level following Paolucci (2010) for the butterflies, and Falk (2019) and Amiet et al. (1996) for the bumblebees. Specimens that could not be identified in the field were collected, transported to the laboratory, and later identified with the aid of a stereoscope.

In line with the approach of previous studies (Goulson et al. 2005; Öckinger et al. 2010), species were classified according to their trophic specialisation, a key trait influencing their sensitivity to habitat changes and restoration measures. Specifically, with respect to butterfly species, we used the specialisation scale proposed by Öckinger et al. (2010), which allows to categorise butterfly species into three classes according to larval specialisation: a) monophagous, when the larva uses only one plant species as a host plant, b) oligophagous, when the larva uses one genus or one family of plants as host plants, and c) polyphagous, when the larva uses

more than one family of plants as host plants. Monophagous and oligophagous that use one genus of plants have been considered as specialist species, while oligophagous using one family of plants and polyphagous have been considered as generalist species (Table S3). Bumblebee species were classified after Goulson et al. (2005), which categorise the species based on proboscis length, as a proxy for the ability to feed on specific floral morphologies. Accordingly, bumblebee species with proboscises longer than 9 mm have been considered as specialist species, while species with medium (8 – 9 mm) or short (≤ 8 mm) proboscises have been classified as generalists (Table S3).

Data analysis

To investigate the effect of restoration measures on butterfly and bumblebee communities across the two sampling years (2022 and 2023), we calculated the difference in species richness and abundance between the two years (2023-2022) for each sub-transect and each month sampled. A constant variable, C (set to a value ensuring all $y + C$ are positive), was added to have only positive values and the data were normalised by $\log_{10}$ -transforming the argument ($\log(y + c)$).

To assess the influence of restoration area (i.e., relative amount of restored area) and landscape composition (i.e., urban, agricultural, and seminatural relative surface cover) on the variation in species richness and abundance of butterflies and bumblebees ($\Delta_{2023-2022}$ butterfly abundance (ΔBA), $\Delta_{2023-2022}$ butterfly species richness (ΔBSR), $\Delta_{2023-2022}$ bumblebee abundance (ΔBBA), $\Delta_{2023-2022}$ bumblebee species richness ($\Delta BBSR$)) in restored and unrestored sub-transects, we evaluated a total of 16 Linear Mixed Models (LMMs) corresponding to each dependent variable, set of independent variables and sub-transect combination. To avoid multicollinearity and ensure analytical robustness, we restricted our analysis to total species richness and total abundance as dependent variables, rather than assessing specialists and generalists separately, as this provides a more stable and interpretable measure of community-level change. This decision was based on two considerations. First, the extremely low richness and abundance of specialist species per transect resulted in insufficient variance to allow reliable parameter estimation in separate models. Second, the species richness and abundance of generalists of both butterflies and bumblebees were highly collinear with total species richness and abundance (Pearson's $r > 0.7$), reflecting their numerical dominance in the analysed communities. As total species richness and abundance is the composite sum of generalist and specialist species, such collinearity would affect the interpretability of the independent effects attributed to each group.

Potential collinearity between independent variables was assessed using Pearson's rank correlation, and linearly independent variables were retained (absolute value of Pearson's $r < 0.7$). Due to the strength of the association between urban and agricultural land cover across all two buffer extents, and because the farms were located in predominantly agricultural contexts, urban land cover was excluded from the models. Individual surveys were treated as replicates, with farm and sub-transect identities included as random factors in the models. Using a stepwise backward selection, we eliminated the non-significant variables from the model at each step until only terms with $P < 0.05$ remained in the model. All models were generated using R version 4.2.2 with lme4 package (lmer function; R Development Core Team 2022).

Results

During the two-year sampling period, a total of 32 butterfly species with 2,451 individuals, and 9 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 S3). Among the bumblebees, the most abundant species was *Bombus pascuorum* (272 individuals), followed by *B. terrestris* (136 individuals) and *B. hortorum* (46 individuals) (Table S3). For both butterflies and bumblebees, the species pool was dominated by generalist species (94% and 67% of observations, respectively).

Overall, the abundance of individuals of both pollinator groups increased between 2022 and 2023 (Table 1). In contrast, species richness remained relatively stable, often showing only species turnover between sampling years (Table 1; Table S3). In terms of trophic specialisation, the increase in individual abundance in both butterflies and bumblebees was primarily driven by generalist species (Table 1; Table S3).

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 54.14% and 68.15% of sub-transects, respectively. For bumblebees, species richness increased in 50.95% of sub-transects, while abundance increased in only 43.31% of sub-transects, with neutral responses observed in 48.40% of sub-transects. In unrestored sub-transects, butterflies responded positively overall (with an increase in species richness and abundance in 54.16% and 68.75%, respectively), while the increase in species richness for bumblebees was observed in only 44.79% of sub-transects and decreased to 33.33% when considering abundance. Moreover, the neutral responses were comparable (44.79% for species richness) or even higher (58.85% for abundance) than the positive responses.

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

The influence of restoration measures and landscape composition on pollinator responses varied at different spatial scales (200 metres and 600 metres buffers), between the different sub-transect types (restored vs. unrestored) and between the different pollinator taxa (butterflies vs. bumblebees), as summarised in Table 2. At the local scale (i.e., 200 metres buffer), butterfly richness and abundance in the restored sub-transects were positively associated with the relative amount of the restored area, suggesting that the restoration measures

significantly improved butterfly communities (Table 2; Figure 1a–b). In the unrestored sub-transects, butterfly and bumblebee abundance increased significantly with the relative amount of the restored area, suggesting possible spillover effects from nearby restored habitats. In addition, butterfly species richness in the unrestored sub-transects was positively related to the relative cover of agricultural and semi-natural habitats (Table 2; Figure 1c–f), suggesting that a structurally heterogeneous landscape supports a larger species pool of butterflies. No significant relationship was found between butterfly richness and abundance and landscape composition in restored sub-transects, suggesting that the amount of restored area exerts a stronger influence than landscape composition. Moreover, no significant relationship was found between the relative amount of the restored area and landscape composition and the richness and abundance of bumblebees in the restored sub-transects or the species richness of bumblebees in the unrestored sub-transects.

At the landscape scale (i.e., 600 metres buffer), butterfly abundance was positively related to the relative cover of agricultural and semi-natural habitats, whereas species richness responded positively to the relative amount of the restored area (Table 2; Figure 2a–c). In the unrestored sub-transects, both butterfly abundance and species richness increased with the relative amount of the restored area, emphasising the benefits of local restoration measures at a broader landscape scale (Figure 2d–e). No significant relationship was found between butterfly richness and landscape composition or between the relative amount of restored area and butterfly abundance in the restored sub-transects, and between butterfly richness and abundance and landscape composition in the unrestored sub-transects.

In addition, no significant relationships were found between the richness and abundance of bumblebees at landscape scale in either the restored or unrestored sub-transects. This indicates a more limited sensitivity of bumblebees to the restoration measures and landscape composition at a broader spatial scale

Table 1: Total specialist and generalist butterfly and bumblebee species richness and abundance recorded during the two sampling years (2022, 2023). The classification of generalist species followed Öckinger et al. (2010) for butterfly species and Goulson et al. (2005) for bumblebee species (Table S3).

Pollinator group	Dep. Variable	2022		2023	
		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

Table 2: Statistics regarding the difference in butterfly (ΔBA) and bumblebee abundance (ΔBBA), and butterfly species richness (ΔBSR) in relation to in relation to the percentage of restored area, agricultural land, and seminatural area. Results are organized organised by buffer size (200m and 600m). Only statistically significant results are reported.

Dep. variable	Indep. variable	Est. coeff.	SE	<i>Z-score</i>	<i>P</i>	χ^2	Significance
200 metres buffers							
Restored sub-transects ($\geq 75\%$ of the sub-transect traverses restored area)							
ΔBA	% restored area	0.021	0.006	3.520	<0.001	11.038	***
ΔBSR	% restored area	0.030	0.009	3.271	0.002	9.711	**
Unrestored sub-transects (< 75% of the sub-transect traverses restored area)							
ΔBA	% restored area	0.021	0.009	2.459	0.014	6.015	*
ΔBSR	% agricultural land	0.002	0.001	2.618	0.009	6.839	**
ΔBSR	% seminatural area	0.005	0.003	1.991	0.046	3.987	*
ΔBBA	% restored area	0.014	0.006	2.328	0.021	5.336	*
600 metres buffers							
Restored sub-transects ($\geq 75\%$ of the sub-transect traverses restored area)							
ΔBA	% agricultural land area	0.002	0.001	2.883	0.005	8.004	**
ΔBA	% semi-natural area	0.004	0.002	2.293	0.021	5.321	*
ΔBSR	% restored area	0.238	0.077	3.079	0.003	8.747	**
Unrestored sub-transects (< 75% of the sub-transect traverses restored area)							
ΔBA	% restored area	0.175	0.052	3.369	<0.001	11.137	***
ΔBSR	% restored area	0.156	0.075	2.083	0.037	4.337	*

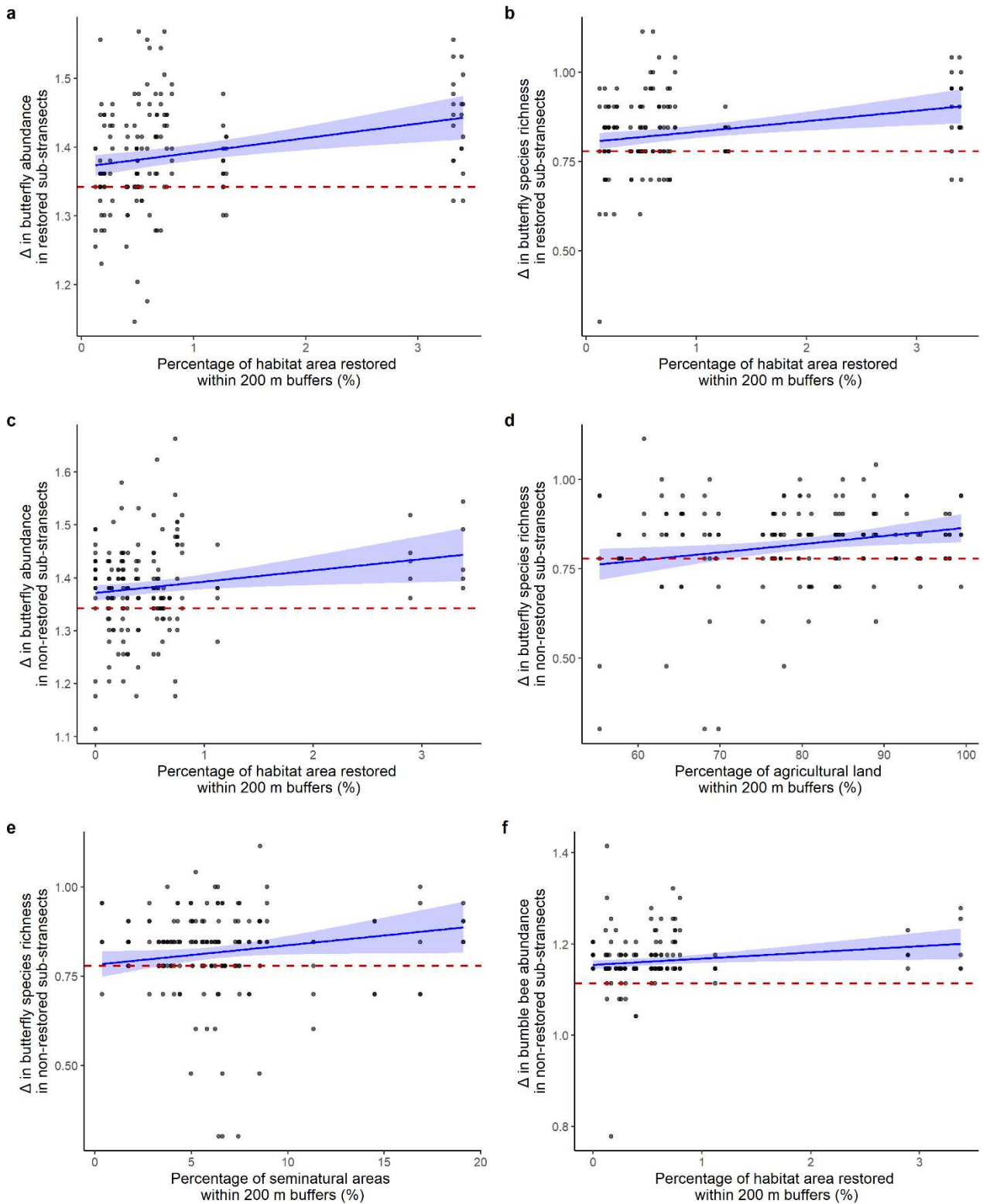


Figure 1: Linear Mixed Models (LMMs). Black dots are original data points. Blue bands represent 95% confidence intervals around regression lines. Red horizontal lines represent zero-values for differences between the two sampled years. Only significant results are included.

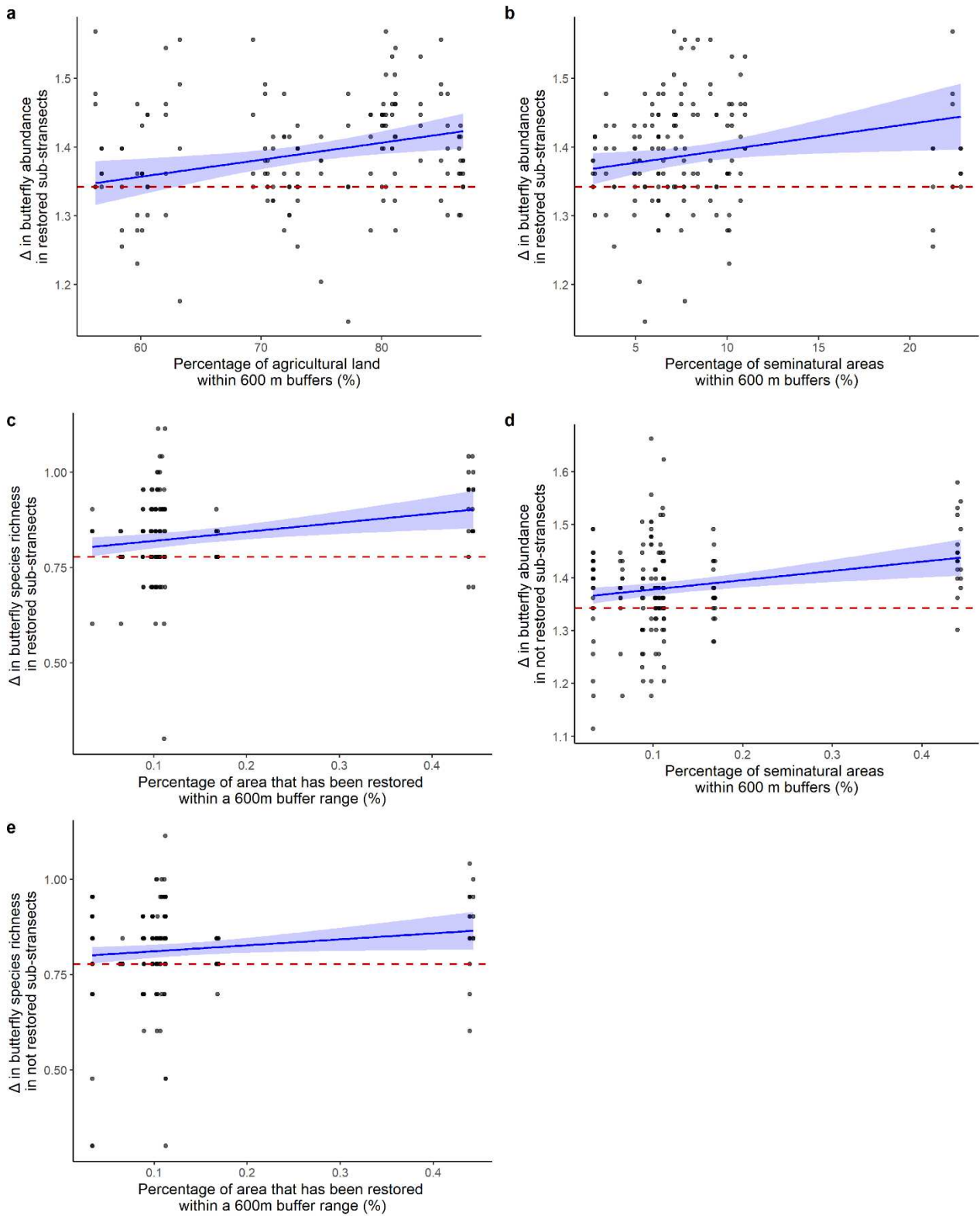


Figure 2: Linear Mixed Models (LMMs). Black dots are original data points. Blue bands represent 95% confidence intervals around regression lines. Red horizontal lines represent zero-values for differences between the two sampled years. Only significant results are included.

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 improves pollinator communities. This finding is consistent with the well-documented impact of habitat loss as a major driver of global biodiversity decline, negatively affecting numerous species, including pollinators (Hogue & Breon 2022). 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 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, the effects of habitat restoration were not consistent between the two target pollinator groups. Butterfly populations responded positively, with species richness and abundance significantly higher in both restored and unrestored sub-transects. In contrast, bumblebee species richness and abundance showed no clear association with the relative amount of restored areas. Previous studies have reported similar inconsistent responses in bumblebee populations (e.g., Le Féon et al. 2010; Redhead et al. 2016; Timberlake et al. 2020). This discrepancy likely reflects differences in resource requirements, mobility and specialisation in nesting and overwintering habitats between the two groups. Bumblebees are known for their ability to rapidly colonise 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 (Osborne et al. 1999; Westphal et al. 2006; Rao et al. 2019). However, in temperate regions, the majority of bumblebees is considered as 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 & Tschamntke 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 relative amount of restored areas.

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. 2019; Potts et al. 2024). Unlike bumblebees, whose high mobility and foraging behaviour may buffer them from local environmental changes, butterflies often exhibit narrower ecological requirements and greater sensitivity to habitat fragmentation and plant composition, and microclimatic conditions. Because butterflies respond to both local habitat conditions and broader landscape-scale changes, they provide a multiscale perspective particularly useful in assessing the effectiveness of restoration interventions (Shuey et al. 2017). In our study, the clear and consistent increase in butterfly richness and abundance in response to restoration, including potential spillover into adjacent areas, underscores their capacity to reflect ecological improvements more sensitively than bumblebees.

Interestingly, restoration benefits were more evident for generalist species, especially within the Pieridae and Lycaenidae families. This pattern aligns with previous research indicating that restoration in intensively managed landscapes tends to favour mobile, generalist species over specialists (e.g., Komonen et al. 2004;

Börschig et al. 2013). Indeed, the composition of the regional species pool is a crucial factor in determining which species can successfully colonise 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 or suitable nectar-producing plants and microhabitats (Öckinger et al. 2010; Curtis et al. 2015).

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 contribute to population improvements in nearby unrestored sub-transects. These results suggest potential spillover effects (Morandin & Kremen 2013; M'Gonigle et al. 2015), although our analysis cannot conclusively demonstrate this mechanism. Spillover typically occurs when restored or natural habitats act as source areas, exporting individuals into surrounding less suitable habitats (Öckinger et al. 2018). In our case, this pattern was especially evident at local scales (200 m), further supporting the role of spatial proximity in facilitating pollinator movement.

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). Notably, butterfly species richness was positively associated with the surrounding landscape even at local scales, suggesting potential colonisation dynamics from adjacent areas. At broader scales, these effects were amplified, reinforcing the idea that source populations of pollinators often originate from beyond the immediate boundaries of restored patches (Lindborg et al. 2017).

Notably, agricultural areas themselves also contributed to pollinator richness, likely due to the presence of synanthropic generalists (e.g., *Pieris* spp.) that can exploit cultivated areas and ruderal field margins as alternative habitats (Harvey & Wagenaar 2006). These species perceive the agricultural matrix as less hostile compared to specialist taxa, which are often more sensitive to habitat degradation (Tschardt et al. 2012; Senapathi et al. 2015). This observation suggests that even an agricultural context may contribute to pollinator movement and persistence in ways that depend on species-specific traits and functional group characteristics (Hass et al. 2018).

In conclusion, our study supports the value of butterflies as more reliable indicators than bumblebees for assessing habitat quality and ecological restoration outcomes, as they have been shown to be more directly influenced by 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 EU Restoration Law (European Union 2024), which calls for the establishment of standardised 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 emphasises 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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Supplementary materials

The study area is characterised by a subhumid continental climate with an average annual precipitation of 850 mm (Berti et al. 2014). The average annual temperature ranges between 10 °C and 14.4 °C. The average minimum temperature in the coldest month of the year (January) is -1.5 °C, while the average maximum temperature in the warmest month of the year (July) is 27.2 °C (Masin et al. 2010). The soil composition is predominantly silty clay, formed by the accumulation of alluvial material transported by the region's rivers (Regione Veneto 2005).

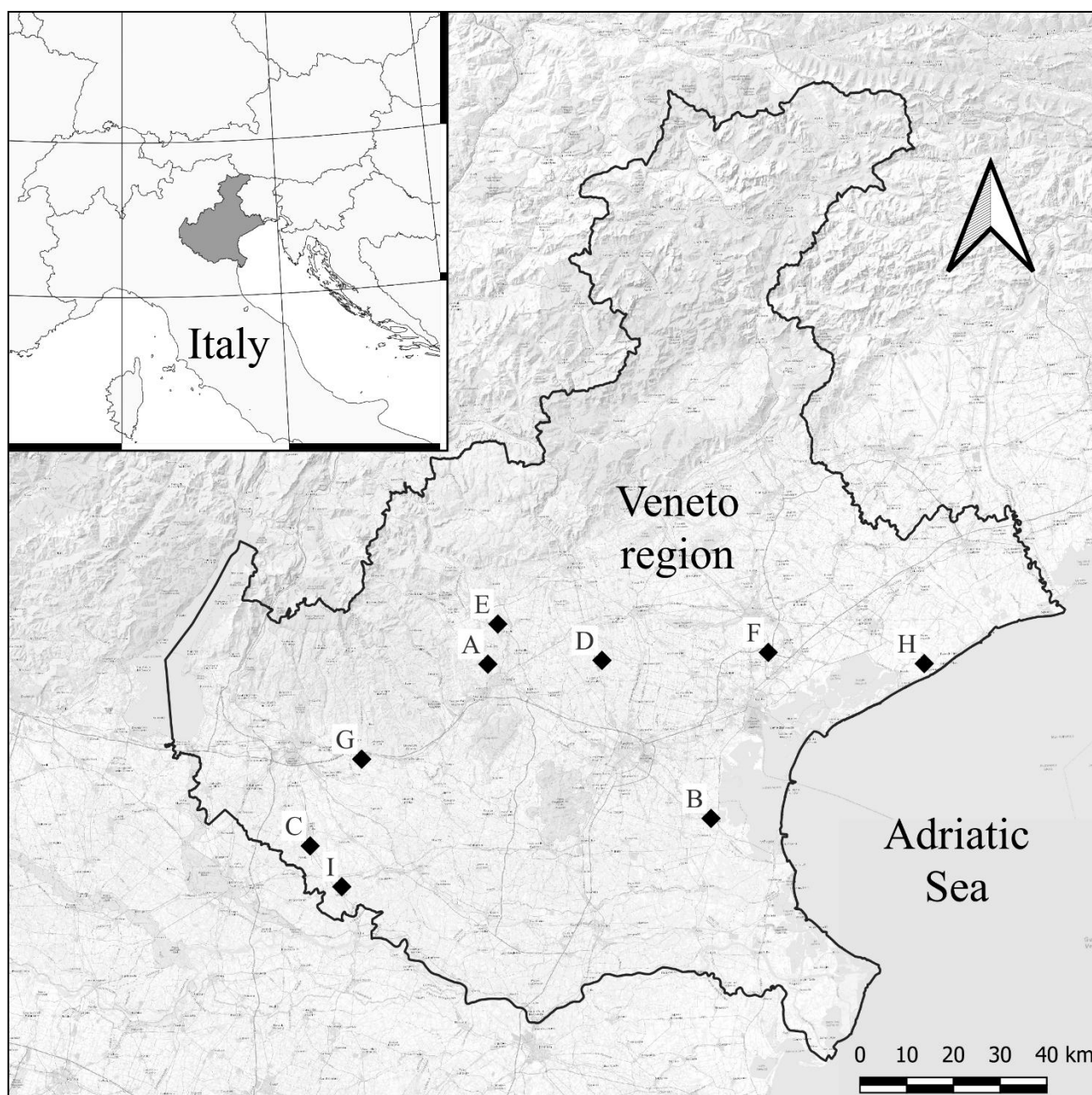


Figure S1: Study region and selected sampled farms.

Table S1: List of species used in restoration measures. Habitat type - habitat type created and/or restored: HM = mesophilous hay meadow; FS = mesophilous flower strip; WFS = hygrophilous flower strip; H/SP = hedgerow and shrub patches. Flowering Period - describes the average flowering duration (in month) in the study area. Life cycle - P = perennial; B = biennial. Plant species nomenclature follows Bartolucci et al. 2024.

Habitat type	Species	Flowering Period (months)	Life cycle
HM/FS	<i>Achillea roseo-alba</i>	May-October	P
HM/FS	<i>Ajuga reptans</i>	December-June	P
WFS	<i>Althea officinalis</i>	April-August	P
WFS	<i>Caltha palustris</i>	February-June	P
WFS	<i>Carex acuta</i>	March-June	P
WFS	<i>Carex vulpina</i>	March-July	P
HM/FS	<i>Centaurea nigrescens</i>	May-December	P
FS	<i>Cichorium intybus</i>	June-November	P
FS	<i>Cirsium arvense</i>	April-November	P
WFS	<i>Cirsium canum</i>	May-September	P
WFS	<i>Cirsium oleraceum</i>	May-September	P
H/SP	<i>Cornus mas</i>	January-April	P
FS	<i>Daucus carota</i>	April-October	B
FS	<i>Echium vulgare</i>	March-September	B
WFS	<i>Eupatorium cannabinum</i>	July-October	P
FS	<i>Hypericum perforatum</i>	April-August	P
WFS	<i>Jacobaea paludosa</i>	May-September	P
HM/FS	<i>Knautia arvensis</i>	April-September	P
HM/FS	<i>Leontodon hispidus</i>	May-October	P
HM/FS	<i>Leucanthemum vulgare</i>	February-October	P
WFS	<i>Lythrum salicaria</i>	May-September	P
FS	<i>Malva alcea</i>	May-September	P
WFS	<i>Mentha longifolia</i>	May-October	P
HM/FS	<i>Ranunculus acris</i>	January-November	P
HM/FS	<i>Salvia pratensis</i>	April-August	P
HM/FS	<i>Scabiosa triandra</i>	May-September	P
HM/FS	<i>Tragopogon orientalis</i>	May-August	P
WFS	<i>Valeriana dioica</i>	April-July	P

Table S2: Mean percentage (%) and standard deviation of CLC classes and restored area within analysed buffers (200 and 600 m) for each sampled farm.

Site ID	CLC class	Mean percentage area (%)	Mean percentage area (%)	Main crop destination
		and standard deviation within 200 metres buffers	and standard deviation within 600 metres buffers	
A	CLC 1	14.294 ± 5.376	20.95 ± 0.901	Cereals
	CLC 2	78.437 ± 4.111	70.909 ± 0.784	
	CLC 3	5.607 ± 0.901	6.454 ± 0.522	
	CLC 5	1.05 ± 0.725	0.852 ± 0.039	
	Restored area	0.612 ± 0.149	0.836 ± 0.949	
B	CLC 1	9.919 ± 3.727	13.716 ± 2.696	Cereals
	CLC 2	73.812 ± 11.795	73.951 ± 4.155	
	CLC 3	10.189 ± 4.205	7.511 ± 0.979	
	CLC 5	5.833 ± 5.761	4.734 ± 0.647	
	Restored area	0.247 ± 0.085	0.088 ± 0	
C	CLC 1	35.943 ± 11.147	20.611 ± 3.105	Horticulture
	CLC 2	58.955 ± 11.831	74.286 ± 2.785	
	CLC 3	4.722 ± 1.803	4.884 ± 0.661	
	CLC 5	0 ± 0	0.155 ± 0.364	
	Restored area	0.38 ± 0.134	0.065 ± 0.001	
D	CLC 1	15.094 ± 3.404	12.952 ± 1.029	Horticulture
	CLC 2	77.823 ± 2.495	80.016 ± 0.639	
	CLC 3	6.352 ± 1.094	6.934 ± 0.439	
	CLC 5	0 ± 0	0 ± 0	
	Restored area	0.731 ± 0.032	0.098 ± 0.001	
E	CLC 1	28.965 ± 7.827	19.942 ± 0.56	Horticulture
	CLC 2	60.35 ± 3.178	57.111 ± 1.741	
	CLC 3	10.298 ± 5.047	21.81 ± 1.444	
	CLC 5	0 ± 0	1.025 ± 1.002	
	Restored area	0.387 ± 0.204	0.112 ± 0	
F	CLC 1	20.115 ± 13.195	29.484 ± 0.499	Horticulture
	CLC 2	72.273 ± 14.524	61.338 ± 1.131	
	CLC 3	7.188 ± 3.363	9.075 ± 0.813	
	CLC 5	0 ± 0	0 ± 0	
	Restored area	0.424 ± 0.23	0.103 ± 0.001	
G	CLC 1	4.714 ± 3.186	11.091 ± 0.586	Orchard
	CLC 2	90.897 ± 3.221	85.602 ± 0.79	
	CLC 3	3.579 ± 0.238	3.139 ± 0.356	
	CLC 5	0 ± 0	0 ± 0	
	Restored area	0.811 ± 0.565	0.168 ± 0.001	

H	CLC 1	2.099 ± 2.429	2.652 ± 0.45	Horticulture
	CLC 2	88.657 ± 2.8	86.819 ± 4.967	
	CLC 3	6.752 ± 1.428	8.176 ± 2.661	
	CLC 5	0 ± 0	1.911 ± 2.017	
	Restored area	2.492 ± 1.475	0.441 ± 0.002	
I	CLC 1	9.263 ± 10.935	8.82 ± 1.121	Horticulture - Cereals
	CLC 2	87.315 ± 13.459	87.799 ± 1.342	
	CLC 3	3.269 ± 2.69	3.348 ± 1.015	
	CLC 5	0 ± 0	0 ± 0	
	Restored area	0.153 ± 0.127	0.033 ± 0	

Table S3: Abundance of butterfly and bumblebee species recorded in the two sampling years. Bumblebee and butterfly nomenclature follows Falk (2019) and Paolucci (2010), respectively. Butterfly trophic specialisation follows Öckinger et al. (2010), based on the specialisation of larval host plants, where 1 represents specialist species (oliphagous (within a genus) and monophagous species) and 0 represents generalist species (oliphagous (within a family) and polyphagous species). Bumblebee trophic specialisation follows Goulson et al. (2005), based on proboscis length, where bumblebee species with long proboscis are considered more specialist (1) compared to bumblebee species with medium or short proboscis (0). Species are listed in descending order of total abundance.

Pollinator species	2022	2023	Specialisation / length
Bumble bee	Abundance		of ligula
<i>Bombus argillaceus</i>	0	1	1
<i>Bombus hortorum</i>	3	43	1
<i>Bombus lapidarius</i>	0	1	0
<i>Bombus lucorum</i>	6	22	0
<i>Bombus muscorum</i>	0	4	1
<i>Bombus pascuorum</i>	48	224	0
<i>Bombus ruderalis</i>	2	0	0
<i>Bombus sylvarum</i>	1	2	0
<i>Bombus terrestris</i>	21	115	0
Butterfly			
<i>Aricia agestis</i>	24	66	0
<i>Carcharodus alceae</i>	1	16	0
<i>Celastrina argiolus</i>	3	54	0
<i>Coenonympha pamphilus</i>	37	138	0
<i>Colias crocea</i>	39	117	0
<i>Cupido argiades</i>	2	35	0
<i>Inachis io</i>	2	0	0
<i>Iphiclides podalirius</i>	1	2	0

<i>Issoria lathonia</i>	1	0	1
<i>Lasiommata megera</i>	7	24	0
<i>Leptotes pirithous</i>	10	46	0
<i>Lycaena phlaeas</i>	30	37	1
<i>Maniola jurtina</i>	3	15	0
<i>Melitaea athalia</i>	4	11	0
<i>Melitaea didyma</i>	33	35	0
<i>Melitaea phoebe</i>	4	12	0
<i>Ochlodes sylvanus</i>	75	73	0
<i>Papilio machaon</i>	0	1	0
<i>Pararge aegeria</i>	4	5	0
<i>Pieris brassicae</i>	72	348	0
<i>Pieris napi</i>	25	31	0
<i>Pieris rapae</i>	143	254	0
<i>Plebeius argus</i>	4	0	0
<i>Plebeius argyrognomon</i>	2	1	0
<i>Polygonia c-album</i>	0	2	0
<i>Polyommatus icarus</i>	111	312	0
<i>Pontia edusa</i>	15	15	0
<i>Pyrgus armoricanus</i>	2	8	0
<i>Pyrgus malvoides</i>	18	17	0
<i>Pyronia cecilia</i>	1	0	0
<i>Vanessa atalanta</i>	8	18	0
<i>Vanessa cardui</i>	64	13	0

Chapter 5

Pollinator responses to climate, entomophilous plant diversity, and management regimes in semi-natural meadows

Abstract

Pollination is an essential ecosystem service linked to agroecosystem functioning and agricultural productivity. In the European agricultural landscape, insect pollinators are crucial in ensuring such ecosystem service, yet they face increasing threats from habitat degradation and climate change. Managed hay meadows are semi-natural habitats rich in biodiversity, providing refuge and food sources for various pollinator communities. However, both the abandonment and intensification of management practices threaten these habitats and their associated plant and pollinator communities. This study investigates how hay meadow management regimes and weather variables influence hay meadows' plant and insect pollinator communities. Between 2022 and 2023, 16 hay meadows under three different management regimes (i.e., intensive, extensive and semi-abandoned) were monitored. From the start to the end of the blooming period, monthly surveys recorded entomophilous plant species, floral display abundance, and pollinator species richness and abundance. Statistical analysis was performed to investigate the effect of management practices of meadows as well as weather variables on pollinator communities' phenology, abundance and species richness. Moreover, an analysis of the species fidelity of pollinators in managed meadows was performed. The results indicated that extensive and semi-abandoned hay meadows hosted the highest richness and floral abundance of entomophilous plants, positively impacting pollinator communities. In contrast, intensive management practices limited the availability of floral resources for pollinators. Different orders of pollinators responded distinctly to weather variables, which reflects their varying phenology and habitat utilisation. Overall, temperature positively influenced pollinator activity, although the responses varied among different orders. Indicator species analysis also identified pollinator species that showed strong fidelity to the differently managed meadows. These results highlight the complex relationship between management intensity, weather variability, pollinator phenology, and their habitat utilisation. Our study emphasises the need for diversified meadow management to support pollinator biodiversity in changing environmental conditions.

Keywords: Meadows management, Floral resources, Plant biodiversity, Pollinator phenology, Pollinator biodiversity, Agroecosystems

Introduction

Animal pollination is one of the key ecosystem processes in terrestrial ecosystems; approximately 87.5% of flowering plants are pollinated by animals (Ollerton et al., 2011). Furthermore, approximately 75% of crops globally benefit from animal pollination, mainly by pollinating insects (Bartomeus et al., 2014). Despite its key role in maintaining ecosystem structure and resilience and ensuring agricultural production, animal pollination is currently threatened by several factors (Potts et al., 2010). Two of the main threats to pollinators are habitat loss (Ricketts et al., 2008) and climate change (Descamps, Quinet, et al., 2021; Ogilvie et al., 2017). Especially in Europe, a substantial loss of semi-natural habitats in agricultural landscapes has been observed mainly due to agricultural intensification (Jeanneret et al., 2021). Among these habitats, grasslands and hay meadows are semi-natural habitats that show among the highest levels of biodiversity of entomophilous plants and pollinators (Emanuelsson, 2009; WallisDeVries & Van Swaay, 2009), and their conservation is a prerogative of new policies such as the European Restoration Law (European Union 2024). These semi-natural habitats rely on regular disturbance in the form of mowing (Aarssen, 1989) or grazing (Hejcman et al., 2013). The regular disturbance through mowing or grazing allows the dominant plant species to be controlled in their presence, allowing other subordinate flowering plant species to establish (Armesto & Pickett, 1985). Among the main threats to the conservation of semi-natural habitats is the intensification and abandonment of traditional management practices. Intensification is characterised by the use of fertilisers and agrochemicals, frequent mowing and the planting of species producing high biomass; all factors that generally lead to community homogenisation, with the loss of subordinate plant species, and to the presence of a few plant species, usually grasses, that are resistant to disturbance and fertilisation (Storkey et al., 2012). In turn, management intensification reduces entomophilous plant species and, thus, flower resources for pollinators (Ziaja et al., 2018). An opposite process leading to changes in semi-natural habitats is their abandonment. The abandonment of marginal areas and the loss of extensive agricultural practices lead to plant community succession, characterised by the progressive encroachment of shrub and tree species and the consequent loss of typical grassland plant species (Kimberley et al., 2019). However, grassland abandonment can also lead to an increase in some trophic and nesting resources that favour particular groups of pollinators (Hussain et al., 2018). Both intensification and abandonment lead to changes in the plant community and a consequent change in the availability of resources, such as pollen, nectar, nurse plants and nesting sites, which cascade effects on pollinator communities (Tschardt et al., 2005). Understanding how these two processes affect the availability of resources and associated pollinator communities is crucial to adopting the appropriate management practices to foster biodiversity conservation in agricultural landscapes.

In temperate grasslands and hay meadows, the main pollinators are insects (Fantinato et al., 2019; Lichtenberg et al., 2024), with Hymenoptera, Diptera, Lepidoptera and Coleoptera representing the main orders (Rader et al., 2020). Among these, Hymenoptera and Diptera are the most extensively studied. However, investigations into how plant community features influence their presence have primarily focused on specific subgroups such as wild bees (Tonietto et al., 2017) and hoverflies (Haenke et al., 2009). Lepidoptera also represent another well-studied group of pollinators, although only a few studies have considered them in conjunction with other

taxa (Cusser et al., 2016; Lichtenberg et al., 2024). In contrast, Coleoptera are comparatively less studied, despite being recognised as an important group of pollinators (Rader et al., 2020). Although these taxonomic groups differ in their ecological needs, they all show a widespread decline in both population size and community composition (Ollerton et al., 2011).

Previous studies have shown that resource availability and diversity generally affect pollinator communities (Fuccillo Battle et al., 2021; Kral-O'Brien et al., 2021; Kremen et al., 2018). Several studies have observed that different groups of pollinators respond differently to floral resources, with Hymenoptera showing a general positive effect compared to other orders showing less clear responses (e.g., Gómez-Martínez et al., 2022, He et al., 2022, Horak, 2014). This different response may be due to the different phenology and resource preferences of different groups of pollinators. For example, in the case of the order Lepidoptera, in addition to the flowering resources for the adult, the presence of nurse plants for the larvae is also important (Altermatt & Pearse, 2011).

Climate change introduces additional stressors for plant and pollinator communities, further challenging their conservation. Climate change can affect plant and pollinator communities differently, influencing pollinator and plant distribution, phenology, morphology, foraging behaviour and attractiveness, disrupting their matches (Gérard et al., 2020). For example, periods of low rainfall alternating with extreme events can negatively affect plant growth (Walter, 2020). Periods of drought directly affect the production of flowers and floral resources, reducing the production of nectar and pollen available to pollinators (Descamps, Quinet, et al., 2021; Lawson & Rands, 2019). The amount of flower rewards is also negatively affected by increased temperature (Alquichire-Rojas et al., 2024). The climate also directly affects pollinators; prolonged periods of rain can hinder the flight of pollinators, limiting their trophic activity (Poulsen, 1996). Indeed, the abundance of flying insects, including pollinators, decreases as precipitation hours increase (Poulsen, 1996). Similarly, as insects are ectothermic organisms, temperature directly affects their physiology by making them sensitive to increases in temperature (Buckley, 2022). Different studies have observed how temperature directly affects the abundance of multiple pollinator taxa by altering their trophic activity, body size, and life span (e.g., Bosch et al., 2000, Radmacher & Strohm, 2010, Scaven & Rafferty, 2013). The cascading effects of temperature on pollinator populations affect the pollination process through their visitation rate, reducing the fitness of plant species (Descamps, Jambrech, et al., 2021). Indeed, temperature was found to be a key factor in defining the visitation rate of pollinators, showing a greater presence of pollinators during the warmer months of the year (Arroyo et al., 1985). Whereas milder temperatures early in the season tend to make flowering plant species bloom earlier (Bertin, 2008). All these effects lead to an overall mismatch between pollinators and flowering plants, putting plant and pollinator species at risk of extinction (Gérard et al., 2020). It is essential to tackle the challenges of habitat modification and climate change to conserve pollinators and the ecosystem services they provide.

Considering the importance of hay meadow management in the conservation of plant and pollinator biodiversity and how climate change may affect plant and pollinator communities, the present study aims to assess how meadow management regime and weather variables affect meadow plants and, in turn, pollinator

community composition and phenology. Specifically, we expect different pollinator orders to respond differently to meadow management regimes and weather variables, both directly and indirectly through their effects on plant communities. For example, orders such as Lepidoptera may be more susceptible to meadow management than other orders, as the larval stage is closely linked to the availability of nurse plants in meadows (Wang et al., 2024). Furthermore, we expect the different orders of pollinators to show different relationships with weather variables due to their different phenology. For example, orders of pollinators such as Hymenoptera and Lepidoptera might be favoured by higher temperatures due to their phenology compared to Coleoptera, which tend to be present in colder months. Lastly, we expect different species of pollinators to be differently associated to meadows management regimes, showing different levels of habitat specialisation.

Materials and methods

Study site

The study was conducted within the Natura 2000 site ZPS - IT3260018 ‘Grave e Zone umide della Brenta’. Specifically, the sampling took place within the agroecological park known as “Le Basse del Brenta” (45°41’34.044” N; 11°41’38.2524” E), located within the municipality of Cartigliano, in the province of Vicenza, Veneto region, Italy (Figure S1).

The area covers 45 hectares and consists of a series of hay meadows managed in different ways, enclosed by hedgerows and wooded areas, forming a “bocage” landscape. The climate is predominantly continental, with cold winters and hot summers. The average temperature for the past 5 years (2019–2023) was 14.80 ± 7.42 °C, while the average precipitation was 1105 ± 200 mm (ARPA, 2024). From a geomorphological perspective, the area is characterized by fluvial and alluvial deposits from the Brenta River. The soil is primarily silty, silty-clayey (Gasparetto et al., 2005). The surrounding territory is mainly used for agriculture, with vast stretches of herbaceous and forage crops, divided by hedgerows, small-wooded areas, or poplar plantations. Additionally, there is a widespread presence of industrial and productive areas located on the outskirts of urban centres, which are characterized by a pattern of dispersed urbanization (Lorenzato et al., 2024).

Within the ‘Le Basse del Brenta’ area, three types of hay meadows with different management practices were identified: i) intensive; ii) extensive; and iii) semi-abandoned. Intensive meadows are characterized by three cuts per year during the growing season and fertilization to increase herbaceous biomass production for forage. Extensive meadows are cut twice a year and are not fertilized. Semi-abandoned meadows are marginal areas where mowing occurs sporadically, approximately once every year to control the spread of woody plants.

Data collection

We selected 16 meadows, among which six are intensive, six extensive and four semi-abandoned meadows. For each of them, we placed 2 permanent sampling plots according to a stratified random sampling design of $2\text{ m} \times 2\text{ m}$, for a total of 32 permanent plots (i.e., intensive meadows: 12 permanent plots; extensive meadows: 12 permanent plots; semi-abandoned meadows: 8 permanent plots) (Figure S1). We sampled entomophilous plant and pollinator species in each plot once per month, from April to September in 2022 and 2023, for a total of 12 surveys over the two years. The sampling plots were always surveyed within a two-day period, on the same day. During each survey, in each plot, the list of plant species in bloom was recorded and the number of

floral displays of each flowering species was counted. Depending on the plant species, a floral display consisted of a single flower (e.g., *Ranunculus bulbosus* L.), a flower head (e.g., *Crepis biennis* L.), or a group of flowers that together formed a recognisable visual unit (e.g., *Trifolium pratense* L.) (Hegland and Totland, 2005).

Weather data (i.e., monthly cumulative precipitation and monthly mean temperature) were selected as weather variables that may influence pollinators' phenology and trophic activity (Trøjelsgaard & Olesen, 2013). The data were obtained through analyses conducted by the ARPA meteorological station located in Rosà (VI, Italy), approximately 7 km from the study area. For each month sampled, the mean value of the monthly temperature (C°) and the cumulative value of precipitation (mm) for the month considered were extracted. Arthropod collection was carried out on sunny days with no or minimal wind (Mahon & Hodge, 2022). Contacts between flowering species and flower visitors were recorded for 14 minutes during each survey, divided into two 7-minute periods, from 10 a.m. to 1 p.m. (morning) and from 1 p.m. to 4 p.m. (afternoon), to capture arthropods with varying daily activity patterns (Fantinato et al., 2019). Visitors were classified as pollinators if they made direct contact with the flower's reproductive organs and stayed on the flower for more than 1 second (Hegland & Totland, 2005). Flower visitors were collected and identified in the laboratory to the morphospecies level using Amiet et al. 2001), Paolucci (2010), Chinery (2012), Ball & Morris (2015), and Falk (2019). All samples are stored in the entomological collection of Ca' Foscari University. Plant species nomenclature follows Bartolucci et al. (2024).

Data analysis

To assess differences in pollinator community composition among the three meadows management regimes (i.e. semi-abandoned, extensive, intensive), a non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity was performed (function `metaMDS`; package `vegan`; Oksanen et al., 2015). Prior to analysis, abundance data were Hellinger-transformed to reduce the influence of dominant species (Legendre & Gallagher, 2001).

Differences in community composition were tested using a permutational multivariate analysis of variance (PERMANOVA) with 9999 permutations (function `adonis2`; package `vegan`; Anderson and Ter Braak, 2003). The model included the three meadows management type (i.e. semi-abandoned, extensive, intensive) as a fixed factor. To identify differences between the pairs of meadows management type, pairwise PERMANOVA comparison was performed with 9999 permutations (function `pairwise.adonis2`; package `pairwiseAdonis`; Anderson, 2001). The pairwise analysis applies a permutation scheme and Bray-Curtis dissimilarity to test all pairwise contrasts (Martinez Arbizu, 2020).

To investigate the specialisation of pollinator species to meadows subjected to different management regimes, Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) was performed (function `multipatt`; package `inicspecies`; De Cáceres and Legendre, 2009; De Cáceres et al., 2010) choosing 'r.g' to identify species fidelity to management frequency (i.e., the number of mowing events per year). Only species with P -value < 0.1 were considered specialised for a management frequency (Hart and Chen, 2008; Kumar et al., 2017). Therefore,

habitat-specialist pollinators were defined all those species visiting exclusively one of the three meadows management type.

To investigate the relationship between management frequency (i.e., the number of mowing events per year), weather variables (i.e., temperature and precipitation), richness of entomophilous species, and number of floral displays, and the richness and number of contacts of pollinator orders (i.e., Coleoptera, Diptera, Hymenoptera, Lepidoptera) we performed GLMMs (package lme4). The statistical analysis followed an information-theoretical approach that compares the fit of a set of models without selecting one best single model based on p-values (Anderson & Burnham, 2002). For the purpose of our research, a total of eight global models were created. Four models used as response variable the species richness of each pollinator order (i.e. Coleoptera, Diptera, Hymenoptera, Lepidoptera), while the other four models used as response variable the number of contacts of each pollinator order. Hemiptera and Orthoptera were excluded from the analyses as their presence during sampling was sporadic. For all global models, the continuous explanatory variables were scaled to mean 0 and standard deviation 1 to make slopes comparable (Gelman, 2008). Before creating the global models, possible collinearity was checked between the independent variables using Spearman's rank correlations and retained those variables that were not highly correlated with each other (i.e., Spearman's $|r| > 0.7$). No correlations were found between the variables, which were therefore all used in the models. Plot identity was included as a random factor in the model, as the data collected during all morning and afternoon surveys were used as replicates. Before performing the global models, an overdispersion analysis was carried out. Negative binomial distribution (function glmer.nb, log as link function) was chosen for all pollinator orders as data were overdispersed (dispersion test function; package AER; O'Hara and Kotze, 2010). All global models included species richness of entomophilous plants, number of floral displays, temperature, precipitation, management and year and the interaction between management and species richness of entomophilous plants and management and number of floral displays as explanatory variables. For a summary of the eight global models, see Table S3. Each set of models were ordered based on their second-order Akaike information criterion corrected for small sample size (AICc), with lower values indicating models that better fit the data. For each model of the set, ΔAICc , i.e., the difference between the model AICc and the lowest AICc of the entire set of models (with the best model having $\Delta\text{AICc} = 0$), and the Akaike model weight, which indicates the probability that the model is the best one, were calculated. As an evaluation of the goodness of fit R^2 was estimated. the model-averaged partial coefficient for each explanatory variable using all models within each set and estimated the 95% confidence intervals around model-averaged partial coefficients were calculated. All multi-model analyses were conducted using the R package MuMIn (Barton, 2020). All set of models with $\Delta\text{AICc} < 6$ (Harrison et al., 2018) were presented in the Tab S4:S11. All analyses were performed in R version 4.2.2 (R Development Core Team 2022).

Results

Overall, 66 species of entomophilous plants and a total of 189,584 floral displays were recorded over the two years (Table S1). Extensive meadows exhibited the highest number of entomophilous plant species (52) and floral displays (84,637), followed by semi-abandoned meadows (49 species; 64,163 floral displays) and intensive meadows (29 species; 40,784 floral displays). When comparing the two monitoring years, we found a higher richness of entomophilous species and a higher number of floral displays in 2023 than in 2022, with 59 species and 153,750 floral displays compared to 49 species and 35,834 floral displays. Extensive meadows in 2022 (35 species; 17,885 floral displays) and 2023 (45 species; 66,752 floral displays) consistently had a greater species richness and a higher number of floral displays than semi-abandoned meadows (34 species; 7,801 floral displays in 2022; 42 species; 56,362 floral displays in 2023) and intensive meadows (22 species; 10,148 floral displays in 2022; 19 species; 30,636 floral displays in 2023).

The plant species contributing most to the number of floral displays included *Galium aparine* (38,849), *Veronica chamaedrys* (17,906), *Geranium molle* (15,452), and *Achillea roseoalba* (12,102). However, their contributions varied over the years. In 2023, *Galium aparine* (38,847), *Veronica chamaedrys* (17,898), *Geranium molle* (15,152), and *Ranunculus repens* (9,370) were the, while in 2022 most important contributors were *Taraxacum officinale* (4,406), *Erigeron annuus* (3,858), *Centaurea nigrescens* (3,487), and *Achillea roseoalba* (3,142) (Table S1).

Weather data collected during the two years revealed notable differences. The year 2022 had higher temperatures but lower precipitations compared to 2023 (Table 1). Specifically, 2022 experienced low precipitation levels until July, after which precipitation increased. In contrast, 2023 exhibited two distinct periods of high precipitation, occurring in May and again in July and August (Table 1).

Table 1: Weather variables (i.e. precipitation (mm) and average temperature (C°)) recorded from the weather station of Rosà (VI, Italy) for each sampling month (i.e. April, May, June, August, September) for the two sampling years (2022, 2023).

Climate variables	Year	Month					
		April	May	June	July	August	September
Precipitation (mm)	2022	64.8	57.8	43.8	44.6	131.6	153.8
Temperature (C°)	2022	12.2	20.2	25	27.1	25.5	19.2
Precipitation (mm)	2023	72.8	175.4	114.8	145.8	142.6	43.2
Temperature (C°)	2023	12.6	18.3	23	25.1	25.1	22.1

During the two sampling years, a total of 2,424 contacts between pollinators and entomophilous plants were recorded (Table S2). Extensive meadows exhibited the highest number of contacts (1,117), followed by intensive meadows (738) and semi-abandoned meadows (569). In 2023 a higher number of contacts were recorded (1,411) compared to 2022 (1,013).

Hymenoptera accounted for the greatest species richness (119) and the highest number of contacts (1,326), followed by Diptera (65 species; 523 contacts), Lepidoptera (35 species; 267 contacts), and Coleoptera (13 species; 246 contacts) (Table S2).

Hymenoptera showed similar values of species richness across years (77 in 2022; 75 in 2023), while Diptera (47 in 2022; 32 in 2023), Lepidoptera (23 in 2022; 24 in 2023), and Coleoptera (8 in 2022; 12 in 2023) exhibited variations. Regarding the number of contacts, more Hymenoptera (566 in 2022 compared to 760 in 2023), Diptera (95 in 2022 compared to 328 in 2023), Lepidoptera (121 in 2022 compared to 146 in 2023) and Coleoptera (102 in 2022 compared to 144 in 2023) were recorded in the second sampling year. Extensive meadows supported the highest number of contacts and species richness among all management regimes (Table 2).

The pollinator species that contributed most to the contacts were *Apis mellifera* L. (490), *Bombus pascuorum* Scopoli (234), and *Sphaerophoria scripta* L. (180). These contributions were consistent across years: *Apis mellifera* L. (157 in 2022; 333 in 2023), *Bombus pascuorum* Scopoli (142 in 2022; 92 in 2023), and *Sphaerophoria scripta* L. (75 in 2022; 105 in 2023).

Table 2: Total number of pollinator species and total number of contacts of each pollinator order recorded for each management type of meadows (i.e. semi-abandoned, extensive and intensive).

Order	Semi-abandoned		Extensive		Intensive	
	N° of pollinator species	N° of contacts	N° of pollinator species	N° of contacts	Number of pollinator species	N° of contacts
Hymenoptera	46	293	82	593	55	440
Diptera	24	135	48	265	33	123
Lepidoptera	18	77	27	124	16	66
Coleoptera	9	41	8	112	9	93
Orthoptera	1	14	2	9	2	13
Rhyncota	4	9	8	14	2	3

The NMDS ordination (stress = 0.257, k = 2) revealed patterns of pollinator community differentiation across meadows management regimes, with semi-abandoned and extensive meadows clustering, while intensive meadows represented a distinct cluster in the ordination space (Fig. 1).

The analysis of PERMANOVA showed a significant effect of management regime on pollinator community composition (Table 3). Pairwise comparisons showed that intensive meadows differed significantly from both semi-abandoned and extensive meadows (Table 3). In contrast, communities of semi-abandoned and extensive meadows did not differ significantly (Table 3).

Table 3: Results of PERMANOVA and pairwise PERMANOVA analyses assessing differences in pollinator community composition across grassland management types. The overall PERMANOVA tested for differences among all three management regimes (i.e., semi-abandoned, extensive, intensive). Pairwise comparisons were conducted between each pair of management types. Degrees of freedom, sum of squares, R^2 , pseudo-F statistic, and permutation-based p-values are reported.

	Df	Sum of Squares	R^2	F-value	p-value	Significance
PERMANOVA	1	0.6333	0.0851	2.7892	0.001	***
Pairwise Extensive vs Intensive	1	0.5081	0.0938	2.2759	<0.001	**
Pairwise Extensive vs Semi-abandoned	1	0.2786	0.0630	1.2105	0.170	ns
Pairwise Intensive vs Semi-abandoned	1	0.5993	0.1310	2.7135	<0.001	***

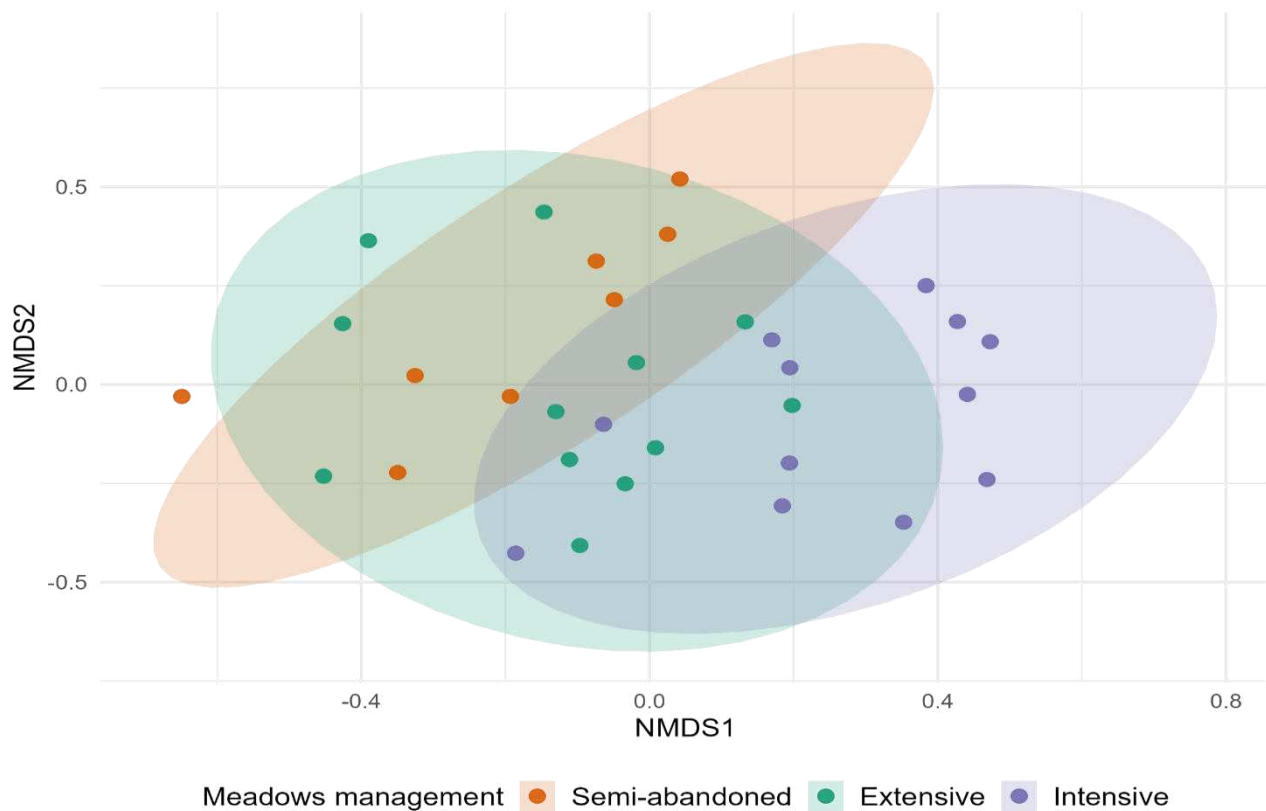


Figure 1: Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity of pollinator communities across grassland management types (i.e., semi-abandoned, extensive, intensive). Each point represents a sampled site. Ellipses indicate the 95% confidence regions around centroids of each management group.

Indicator species analysis revealed a total of 15 pollinator species significantly associated with one or more management regime of meadows (Table 4). Among these, two species were specifically associated with semi-abandoned meadows, including *Heriades truncorum* L. and *Melitaea athalia* Rottemburg. Six pollinator species were significantly associated with extensive meadows, such as *Bombus terrestris* L., *Coenonympha pamphilus* L., and *Bombylius cinerascens* Mikan. Only one pollinator species, *Andrena humilis* Imhoff, was significantly associated with intensive meadows. Additionally, several pollinator species were shared indicators of different management type of meadows (Table 4). Four species, including *Ochlodes sylvanus* Esper and *Formicidae sp1*, were significantly associated with both semi-abandoned and extensive meadows, while *Eristalis tenax* L. and *Colias croceus* Geoffroy were associated with both extensive and intensive meadows (Table 4).

Table 4: Indicator species associated with each management type of meadows (i.e. semi-abandoned, extensive and intensive) according to multilevel pattern analysis (IndVal). Significance was assessed using permutation tests (n = 999). Only species with significant associations (p < 0.1) are shown.

Pollinator species	Management	IndVal value	p-value	Significance
<i>Melitaea athalia</i>	Semi-abandoned	0.640	0.021	*
<i>Heriades truncorum</i>	Semi-abandoned	0.572	0.044	*
<i>Bombylius cinerascens</i>	Extensive	0.707	0.002	**
<i>Coenonympha pamphilus</i>	Extensive	0.674	0.008	**
<i>Stelis phaeoptera</i>	Extensive	0.645	0.014	*
<i>Bombus terrestris</i>	Extensive	0.638	0.048	*
<i>Bombylius venosus</i>	Extensive	0.592	0.048	*
<i>Tachinidae sp7</i>	Extensive	0.500	0.098	.
<i>Andrena humilis</i>	Intensive	0.577	0.024	*
<i>Ochlodes sylvanus</i>	Semi-abandoned + Extensive	0.834	0.003	**
<i>Formicidae sp1</i>	Semi-abandoned + Extensive	0.753	0.027	*
<i>Crisomelidae sp1</i>	Semi-abandoned + Extensive	0.742	0.014	*
<i>Ceratina cyanea</i>	Semi-abandoned + Extensive	0.632	0.036	*
<i>Eristalis tenax</i>	Extensive + Intensive	0.835	0.003	**
<i>Colias croceus</i>	Extensive + Intensive	0.645	0.090	.

For Coleoptera, 29 models exhibited a $\Delta AICc < 6$ for richness of Coleoptera species (Table S4) and 24 models for the number of contacts of Coleoptera (Table S8). Model averaging showed that the species richness of entomophilous plants and temperature influenced both the richness of Coleoptera species and their number of contacts in the meadows. Specifically, species richness of entomophilous plants had a positive effect on richness of Coleoptera species, while temperature showed a negative effect on both response variables (Table 5; Figure 2a; Figure 3a). All other variables and interactions did not significantly influence the richness of Diptera species or the number of their contacts.

For Diptera, 43 models showed a $\Delta AICc < 6$ for richness of Diptera species (Table S5) and 62 models for the number of contacts of Diptera (Table S9). Model averaging showed that only the species richness of entomophilous plants had a significant positive effect on richness of Diptera species and the number of contacts (Table 5; Figure 2b; Figure 3b). All other variables and interactions did not significantly influence the richness of Diptera species or the number of their contacts.

For Hymenoptera, 22 models displayed a $\Delta AICc < 6$ for richness of Hymenoptera species (Table S6) and 12 for the number of contacts of Hymenoptera (Table S10). Model averaging showed that the species richness of entomophilous plants and temperature had a positive effect on both the richness of Hymenoptera species and the number of contacts. Additionally, the categorical variable "year" had a significant negative effect on the number of contacts (Table 5; Figure 2c; Figure 3c). All other variables and interactions did not significantly influence the richness of Diptera species or the number of their contacts.

For Lepidoptera, 32 models exhibited a $\Delta AICc < 6$ for richness of Lepidoptera species (Table S7) and 8 models for the number of contacts of Lepidoptera (Table S11). Model averaging indicated that species richness of entomophilous plants and temperature positively influenced on richness of Lepidoptera species (Table 5; Figure 2d). For the number of contacts, in addition to species richness of entomophilous plants and temperature, the number of floral displays, management, and the interaction between management and floral displays also had significant effects. Specifically, the number of floral displays had a significant positive effect, while management had a significant negative effect on the number of contacts (Table 5; Figure 3d). The interaction between management and floral displays showed a positive effect. All other variables and interactions did not significantly influence the richness of Diptera species or the number of their contacts.

Table 5: Summary of the eight global models. Explanatory variables are Management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023). The continuous explanatory variables were scaled to mean 0 and standard deviation 1 to make slopes comparable.

Dependent variable	Independent variable	Estimated coefficient	SE	z-score	P	Sign. level
Richness of Coleoptera species	Species richness of entomophilous plants	1.064023	0.106019	10.021	<2e-16	***
Richness of Coleoptera species	Temperature	-0.328937	0.090169	3.642	0.00027	***
Number of contacts of Coleoptera	Species richness of entomophilous plants	1.340854	0.146481	9.139	<2e-16	***
Number of contacts of Coleoptera	Temperature	-0.369691	0.118988	3.102	0.00192	**
Richness of Diptera species	Species richness of entomophilous plants	0.950071	0.057334	16.546	<2e-16	***
Number of contacts of Diptera	Species richness of entomophilous plants	1.13060	0.07806	14.462	<2e-16	***
Richness of Hymenoptera species	Species richness of entomophilous plants	1.011e+00	4.399e-02	22.949	< 2e-16	***
Richness of Hymenoptera species	Temperature	3.248e-01	4.291e-02	7.557	<2e-16	***
Number of contacts of Hymenoptera	Species richness of entomophilous plants	1.208671	0.081462	14.814	<2e-16	***
Number of contacts of Hymenoptera	Temperature	0.580993	0.069053	8.400	<2e-16	***
Number of contacts of Hymenoptera	Year 2023	-0.413248	0.169691	2.432	0.015	*
Richness of Lepidoptera species	Species richness of entomophilous plants	0.936415	0.093577	9.991	< 2e-16	***
Richness of Lepidoptera species	Temperature	0.937069	0.124596	7.509	< 2e-16	***
Number of contacts of Lepidoptera	Management	-0.30698	0.11335	2.704	0.00685	**
Number of contacts of Lepidoptera	Number of floral displays	0.35778	0.08532	4.187	2.83e-05	***
Number of contacts of Lepidoptera	Species richness of entomophilous plants	1.01248	0.11773	8.586	< 2e-16	***
Number of contacts of Lepidoptera	Temperature	1.15053	0.14876	7.722	< 2e-16	***
Number of contacts of Lepidoptera	Management*Number of floral visual displays	0.30963	0.06134	5.040	5.00e-07	***

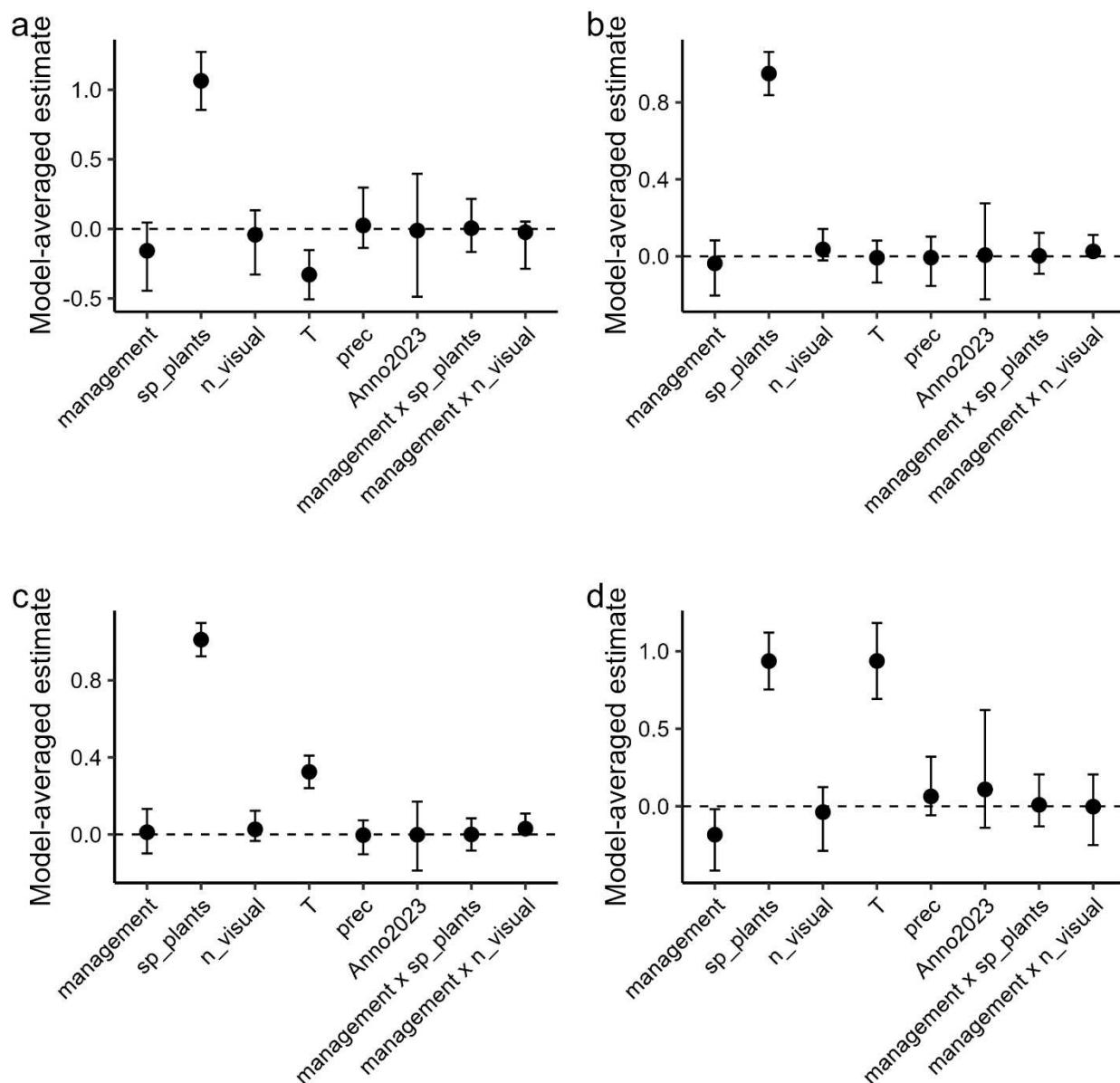


Figure 2: Model estimates from the model-averaging procedure based on the four sets of models considering species richness of pollinator orders, i.e., a) richness of Coleoptera species, b) richness of Diptera species, c) richness of Hymenoptera species, and d) richness of Lepidoptera species. Explanatory variables of the four global models are management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023) and the following interactions: management $\times$ sp_plants and management $\times$ n_visual. All continuous explanatory variables were scaled to mean 0 and standard deviation 1. Dots indicate the model estimated means, while error bars indicate the 95% confidence intervals for the expected values of the variables.

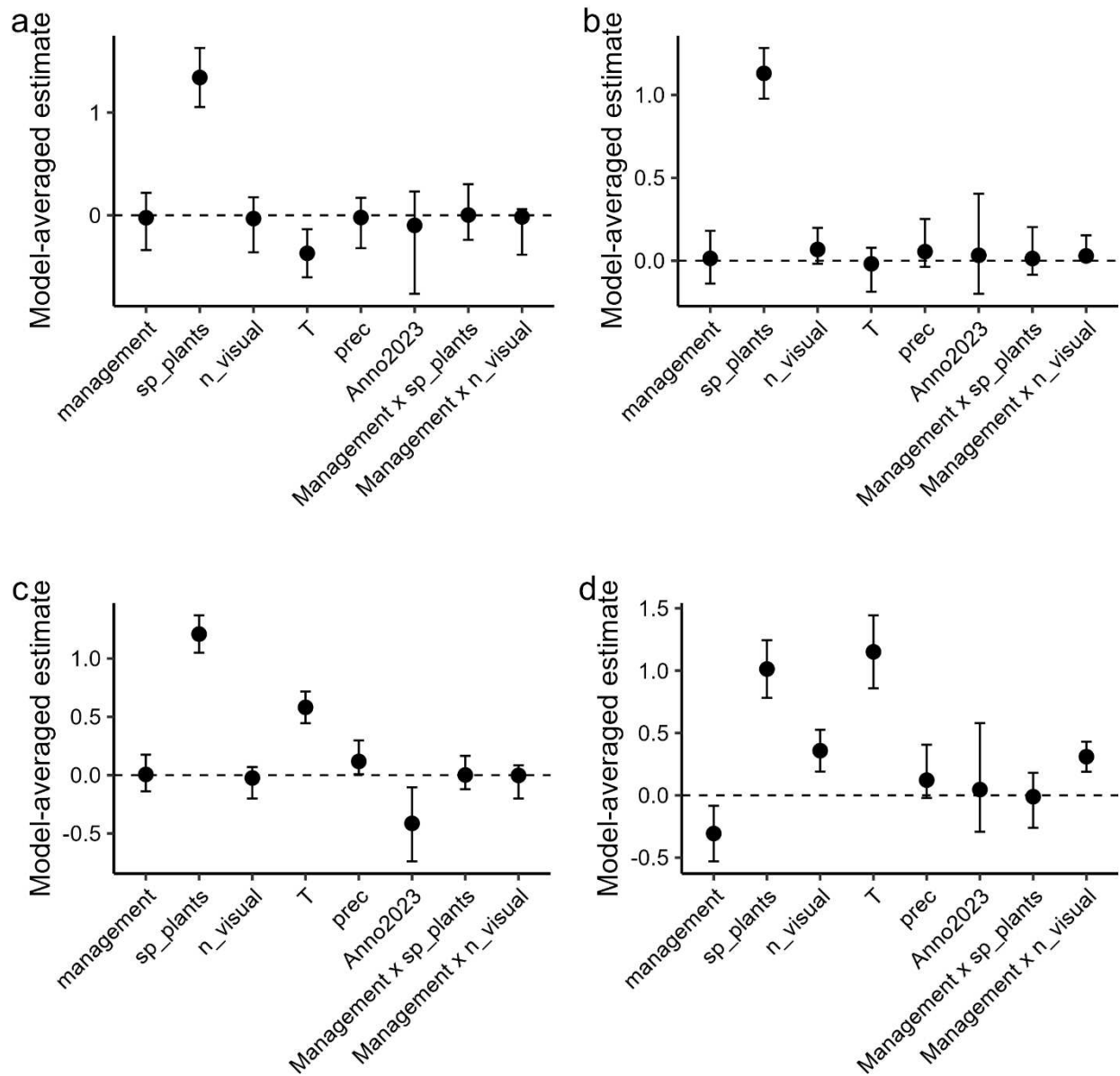


Figure 3: Model estimates from the model-averaging procedure based on the four sets of models considering Number of contacts of pollinator orders, i.e., a) number of contacts of Coleoptera, b) number of contacts of Diptera, c) number of contacts of Hymenoptera, and d) number of contacts of Lepidoptera. Explanatory variables of the four global models are management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management $\times$ sp_plants and management $\times$ n_visual. All continuous explanatory variables were scaled to mean 0 and standard deviation 1. Dots indicate the model estimated means, while error bars indicate the 95% confidence intervals for the expected values of the variables.

Discussion

The study underscores the importance of hay meadow management and weather variables on the distribution and phenology of pollinator communities. From the perspective of the management of the meadows, different management intensity defines the different pollinator communities associated with them. Specifically, the pairwise comparisons indicated that the pollinator communities differed when comparing semi-abandoned and extensive meadows with intensive meadows; conversely, semi-abandoned and extensive meadows did not exhibit significant differences. These findings are in line with previous research that demonstrated that extensive practices and low levels of abandonment of meadows can support different pollinator communities compared to intensively managed meadows (Motivans Švara et al., 2021). Our results are also supported by the analysis of species fidelity and specialisation of pollinators. Although different pollinator species showed high specificity to either extensive or semi-abandoned meadows, some species were also shared between these management types. Only *Andrena humilis* showed a specificity for the intensive meadows, with only *Eristalis tenax* and *Colias croceus* in common with extensive meadows. The specialisation of *Andrena humilis* could be related to the need of this species of wild bees for compacted soil for nest building, probably favoured by the frequent passage of vehicles over intensive meadows (Falk, 2019). *Eristalis tenax* and *Colias croceus* are generalist species both for habitat use and resource needs (Paolucci, 2010; Bot & Meutter, 2023). These findings showed the critical role of diverse management practices in maintaining pollinator biodiversity. Land managers can support specialist pollinator species by preserving a mosaic of semi-abandoned and extensively managed meadows, thereby enhancing the resilience and functionality of pollination services within agricultural landscapes (Fantinato et al., 2019).

From the analysis of weather variables, only mean temperature showed significant relationships with the richness and the number of contacts of pollinators. However, we found contrasting results when considering different orders of pollinators. While Hymenoptera and Lepidoptera showed a positive relationship, Coleoptera were the only order that showed a negative relationship. This result can be explained by the fact that the greatest richness of species and contacts of Coleoptera was observed at the beginning of the season, when temperatures were at their lowest, and then decreased as the season progressed and temperatures rose. In contrast, Lepidoptera and Hymenoptera showed a positive relationship with higher temperatures, hence a greater presence during the warmer months. Similar results have been observed by Rohde & Pilliod (2021), who reported that Lepidoptera and Hymenoptera respond positively to higher temperatures in temperate climates in the middle-late months of the year. Instead, groups of insects that show a hibernal diapause phase, especially as adults, may show an anticipation of their phenology (Hodek, 2012). From the viewpoint of climate change, groups and species of insects that appear to be the first to emerge from diapause could run into several difficulties with current estimates of rising temperatures (Marasco, 2022). In many species, the general principle is that diapause turns out to be shortened with higher temperatures in the winter period (Bale & Hayward, 2010). Several studies have observed how different species and groups of Coleoptera show anticipation of their phenology in the case of little cold winters and milder temperatures in the early spring seasons (Irmeler, 2022; Palvi et al., 2025; Thomsen et al., 2016). This possible anticipation could, in turn, affect

the pollination network level, causing a possible mismatch between flowering plants and pollinators, harming both communities (Scaven & Rafferty, 2013). Despite this, the effects of temperatures on different groups of pollinating insects are still poorly understood due to the complexity of the process (but see López-Urbe et al. (2024) and are often related to single groups of species (e.g., Herrera, 1995, J. G. Holland & Bourke, 2015, Sgolastra et al., 2011). Further studies are needed to understand the phenology of different pollinator groups and to investigate better the possible effects of increased temperatures due to climate change on their phenology.

From our analyses, the species richness of entomophilous plants is an important factor in promoting both species richness and the number of contacts of all pollinator orders studied. This result agrees with the large body of literature that states that greater entomophilous plant richness supports greater pollinator richness and abundance (Ebeling et al., 2008; Kral-O'Brien et al., 2021). Indeed, more diverse entomophilous plant communities ensure greater quantities of floral resources that, in turn, support greater diversity and abundance of pollinators (Dorado & Vázquez, 2014). Generally, more entomophilous species ensure greater separation of trophic niches for pollinators, possibly supporting more pollinators with different trophic needs (Venjakob et al., 2016). Mowing grassland management that promotes plant species richness is thus a helpful management strategy to support pollinators and, thus, pollination service (Orford et al., 2016).

Differences between the different sampling years were found only for Hymenoptera, which showed fewer contacts in 2023 than in 2022 per single plot. Although at the level of the entire two-year sampling period, a higher number of Hymenoptera contacts is observed in 2023, this result can be explained by considering that 2022 showed a lower availability of floral resources, which may have led to a higher concentration of Hymenoptera pollinators on the few available resources. Indeed, when resources are less available, pollinators tend to concentrate on the few available resources (Yahaya et al., 2024). Many of the Hymenoptera found in this study were central pollinators. Central pollinators must travel between the nesting site and the various trophic resources around it, thus defining a limited foraging area (Gathmann & Tscharntke, 2002). This factor limits these pollinators from utilising only those resources close to the nesting site, forcing them to use the floral resources available close to the nest. Moreover, among the various orders of pollinators found, Hymenoptera includes several species that are specialised in using particular entomophilous plant species (Rasmussen et al., 2020). Due to their specialisation, these species can only utilise specific floral resources, concentrating on those available entomophilous plant species (Wcislo & Cane, 1996). The other orders of pollinators are generally less specialised and, not being central pollinators, are less constrained in moving to find the resources they need (Favarin et al., 2022). This aspect indicates that Hymenoptera is a group of pollinators that respond most to the availability of resources in the vicinity of their nesting sites, which are most likely to be adversely affected by management and climatically unfavourable seasons.

Our results showed that only Lepidoptera were directly affected by meadow management. Specifically, our results showed that intensive management had a negative effect on the number of their contacts. On the other hand, the overall availability of resources, i.e., the number of floral displays, positively affected the number of contacts. Interestingly, however, the interaction between management and the number of floral displays

indicates that the effects of management can be mitigated by the presence of floral displays in the meadows. In agreement with several other authors, management plays a key role in favouring certain groups of pollinators (e.g., Batáry et al., 2010, Buri et al., 2014, Tanis et al., 2020). Intensive meadow management, through a more intensive mowing regime, appears to be unfavourable for arthropods, either given by direct mortality from the practice (Humbert et al., 2009) or by removing floral and nesting resources (Cizek et al., 2012). Conversely, less intense cutting regimes may foster greater heterogeneity in the plant community of mowing meadows, thereby enhancing the availability of resources for various pollinators. Our results also indicate that even semi-abandoned mowing lawns can serve as favourable habitats for Lepidoptera. These meadows, while not entirely abandoned, still maintain an ecological succession that favours the herbaceous community, thereby promoting a variety of species and resources for Lepidoptera. This finding suggests that a shift towards less intense cutting regimes could potentially benefit pollinator communities. This effect may be due to the floral resources sought by adult individuals, such as nectar, and the availability of nurse plants for their larval phase. Compared to other orders of pollinators, Lepidoptera is closely linked in their larval phase to the presence of certain plant families or species on which they feed (X. Wang et al., 2024). For example, from our analyses, Lepidoptera species of the genus *Pyrgus spp.* were found in semi-abandoned and extensive meadows, probably given by the large presence of *Potentilla spp.*, their nurse plant genus, in these meadows (Paolucci, 2010). This availability of resources may, therefore, attract more individuals than in intensive meadows. Studies have shown how meadow management can have contrasting effects on different plant and pollinator species (Motivans Švara et al., 2021; Parmentier et al., 2024). Two processes are considered the most threatening to the biodiversity conservation of meadows: the intensification and abandonment of low-management practices (Gustavsson et al., 2011). Given new policies focused on biodiversity and habitat conservation, promoting the preservation of low-intensity management of meadows is crucial to promoting plant and pollinator biodiversity. Promoting meadow management practices that ensure plant species richness and floral resource abundance is important to conserve biodiversity and support various ecosystem services, including pollination (Kruess & Tschardt, 2002). Similarly, semi-abandoned meadows can still support a diversity of plant species and pollinators, enriching the area's total diversity of plant species and pollinators. From the perspective of climate change adaptation, managing these habitats will be of primary importance. Meadows managed with low-intensive practices support more diverse plant communities that are better able to withstand adverse climatic effects and substantial seasonal variations (Korell et al., 2024). Moreover, meadow cutting regimes that promote later cuts early in the season might favour trophic resources for those groups of wintering pollinators that need resources early in the season (Ammann et al., 2024).

This study highlights how weather variables, management practices, and floral resource diversity affect pollinator taxonomic orders. From this study, it was possible to observe that Coleoptera are mainly present early in the season compared to Hymenoptera and Lepidoptera, suggesting how this group of pollinators might be more affected by the effects of climate change and anticipation of plant flowering. Furthermore, it was possible to identify how meadow management affects different pollinator groups and that semi-abandoned meadows may be critical for conserving pollinator groups such as Lepidoptera. Additionally, the following

study confirmed the critical role of entomophilous plant species richness in fostering pollination diversity and presence, further underscoring the need to promote meadow management practices that promote diverse meadow plant communities. Overall, this research enhances our understanding of the interactions between climate variables and management practices in shaping pollinator communities. Further studies should investigate the interaction between climate variables and the management of these important semi-natural habitats to develop better managements that ensure the sustainability of pollination services in changing agricultural landscapes.

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Supplementary materials

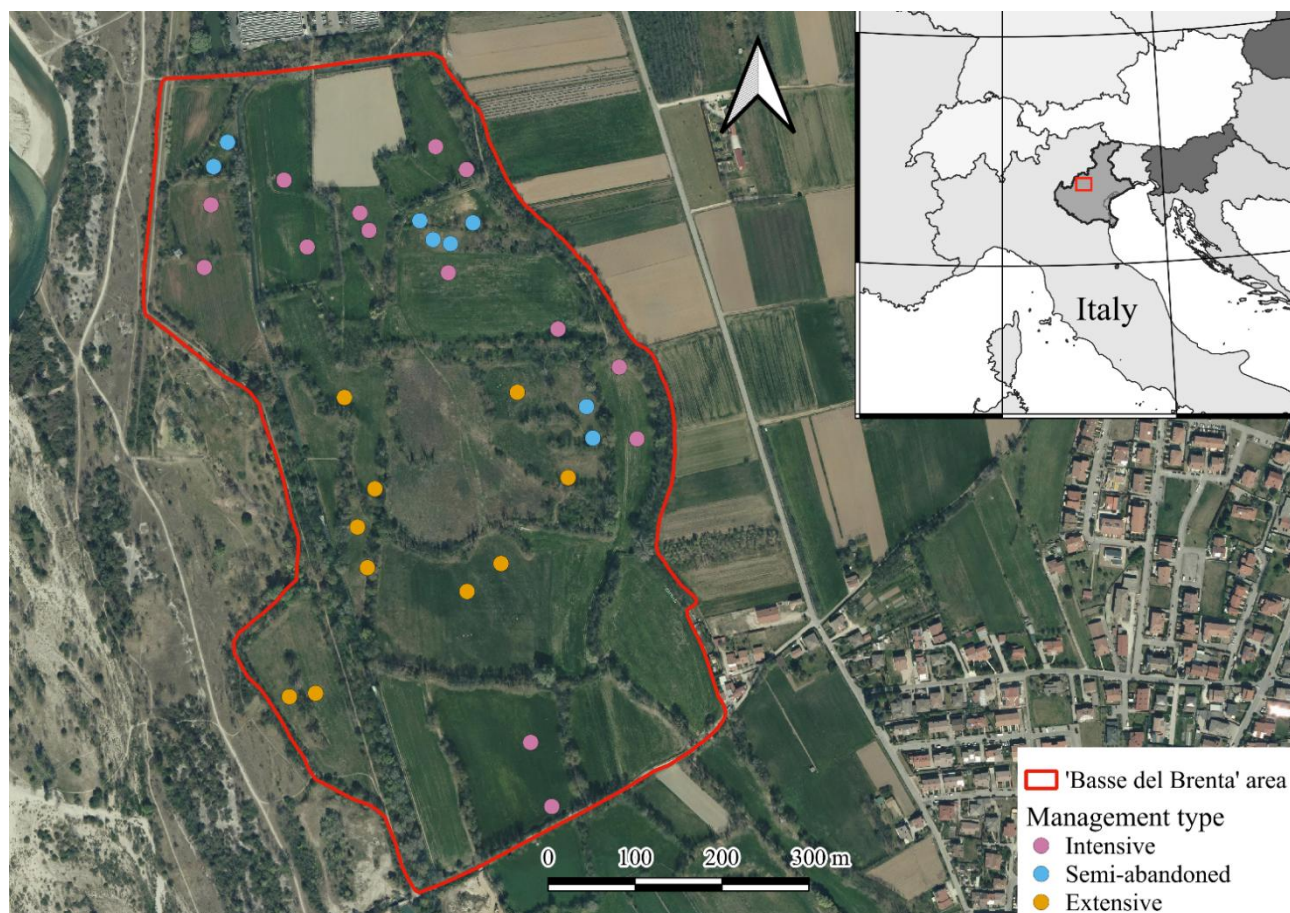


Figure S1: Study region and 'Basse del Brenta' area. Observation sampling points are reported.

Table S1: Entomophilous plant species and number of floral visual display recorded. Plant species nomenclature follows Bartolucci et al. (2024).

Plant species	Number of floral visual display
<i>Achillea millefolium</i>	36
<i>Achillea roseoalba</i>	12102
<i>Agrimonia eupatoria</i>	54
<i>Ajuga reptans</i>	1285
<i>Bellis perennis</i>	84
<i>Capsella bursa-pastoris</i>	3652
<i>Cardamine hirsuta</i>	688
<i>Centaurea nigrescens</i>	4110
<i>Centaureum erythraea</i>	942
<i>Cerastium glomeratum</i>	1762
<i>Cerastium glutinosum</i>	326
<i>Cerastium semidecandrum</i>	74
<i>Clinopodium nepeta</i>	790
<i>Clinopodium vulgare</i>	1772
<i>Convolvulus arvensis</i>	118
<i>Crepis autumnalis</i>	204
<i>Crepis biennis</i>	3162
<i>Daucus carota</i>	8
<i>Erigeron annuus</i>	4307
<i>Erigeron canadensis</i>	4
<i>Erigeron philadelphicus</i>	7302
<i>Ficaria verna</i>	10
<i>Galium album</i>	3782
<i>Galium aparine</i>	38849
<i>Galium mollugo</i>	9400
<i>Geranium dissectum</i>	322
<i>Geranium molle</i>	15452
<i>Geum urbanum</i>	2
<i>Hypericum perforatum</i>	352
<i>Lamium purpureum</i>	964
<i>Leucanthemum vulgare</i>	28
<i>Lotus corniculatus</i>	3439
<i>Lychnis flos-cuculi</i>	1403
<i>Lythrum salicaria</i>	114
<i>Matricaria chamomilla</i>	40
<i>Medicago lupulina</i>	1157
<i>Myosotis arvensis</i>	1646
<i>Oenothera stueckii</i>	57
<i>Ornithogalum umbellatum</i>	84
<i>Oxalis corniculata</i>	231
<i>Oxalis dillenii</i>	64
<i>Oxalis stricta</i>	97
<i>Plantago lanceolata</i>	282
<i>Polygonum aviculare</i>	8
<i>Potentilla reptans</i>	3077
<i>Ranunculus acris</i>	1419

Plant species	Number of floral visual display
<i>Ranunculus bulbosus</i>	2140
<i>Ranunculus repens</i>	9382
<i>Rorippa sylvestris</i>	36
<i>Salvia pratensis</i>	2419
<i>Sherardia arvensis</i>	418
<i>Silene latifolia</i>	12
<i>Silene vulgaris</i>	600
<i>Stellaria media</i>	5280
<i>Taraxacum officinale</i>	5586
<i>Torilis arvensis</i>	225
<i>Trifolium campestre</i>	6
<i>Trifolium pratense</i>	4059
<i>Trifolium repens</i>	4230
<i>Valerianella locusta</i>	2164
<i>Verbena officinalis</i>	1754
<i>Veronica arvensis</i>	4046
<i>Veronica chamaedrys</i>	17906
<i>Veronica persica</i>	4080
<i>Veronica serpyllifolia</i>	68
<i>Vicia sativa</i>	112

Table S2: Orders, morphospecies, and number of contacts for each pollinator recorded.

Order	Pollinator morphospecies	Number of contacts
Coleoptera	<i>Chrysomelidae sp1</i>	35
Coleoptera	<i>Chrysomelidae sp2</i>	2
Coleoptera	<i>Diabrotica virgifera</i>	1
Coleoptera	<i>Milichiidae sp1</i>	2
Coleoptera	<i>Mordellidae sp1</i>	9
Coleoptera	<i>Nitidulidae sp1</i>	34
Coleoptera	<i>Oedemera nobilis</i>	45
Coleoptera	<i>Oxythyrea funesta</i>	31
Coleoptera	<i>Phaedon armoraciae</i>	1
Coleoptera	<i>Phytoecia pustulata</i>	1
Coleoptera	<i>Stictoleptura cordigera</i>	1
Coleoptera	<i>Tropinota hirta</i>	14
Coleoptera	<i>Tropinota squalida</i>	70
Diptera	<i>Agromyzidae sp1</i>	1
Diptera	<i>Anthomyiidae sp1</i>	1
Diptera	<i>Anthomyiidae sp2</i>	2
Diptera	<i>Anthomyiidae sp3</i>	6
Diptera	<i>Bacca elongata</i>	1
Diptera	<i>Bombylius cinerascens</i>	9
Diptera	<i>Bombylius major</i>	60
Diptera	<i>Bombylius venosus</i>	9
Diptera	<i>Brachycera sp1</i>	1
Diptera	<i>Calliphoridae sp1</i>	2
Diptera	<i>Calliphoridae sp2</i>	1

Order	Pollinator morphospecies	Number of contacts
Diptera	<i>Cheilosia ranunculi</i>	1
Diptera	<i>Chloropidae sp1</i>	3
Diptera	<i>Chloropidae sp2</i>	4
Diptera	<i>Chloropidae sp3</i>	1
Diptera	<i>Conopidae sp1</i>	1
Diptera	<i>Conopidae sp2</i>	1
Diptera	<i>Conopidae sp3</i>	1
Diptera	<i>Drosophila sp1</i>	3
Diptera	<i>Empididae sp1</i>	2
Diptera	<i>Empididae sp2</i>	4
Diptera	<i>Empididae sp3</i>	2
Diptera	<i>Epeolus cruciger</i>	1
Diptera	<i>Ephydriidae sp1</i>	1
Diptera	<i>Episyrphus balteatus</i>	43
Diptera	<i>Eristalinus aeneus</i>	1
Diptera	<i>Eristalis arbustorum</i>	13
Diptera	<i>Eristalis tenax</i>	41
Diptera	<i>Eupeodes corollae</i>	1
Diptera	<i>Eupeodes luniger</i>	1
Diptera	<i>Helophilus pendulus</i>	1
Diptera	<i>Helophilus trivittatus</i>	8
Diptera	<i>Melanostoma mellinum</i>	11
Diptera	<i>Merodon avidus</i>	2
Diptera	<i>Milichiidae sp1</i>	1
Diptera	<i>Milichiidae sp2</i>	1
Diptera	<i>Muscidae sp1</i>	1
Diptera	<i>Myathropa florea</i>	2
Diptera	<i>Myopa buccata</i>	2
Diptera	<i>Paragus haemorrhous</i>	1
Diptera	<i>Parasyrphus punctulatus</i>	2
Diptera	<i>Phoridae sp1</i>	1
Diptera	<i>Pipizella viduata</i>	4
Diptera	<i>Platycheirus albimanus</i>	1
Diptera	<i>Sarcophaga sp1</i>	6
Diptera	<i>Scathophagidae sp1</i>	7
Diptera	<i>Scatopsidae sp1</i>	1
Diptera	<i>Sphaeroceridae sp1</i>	14
Diptera	<i>Sphaerophoria scripta</i>	180
Diptera	<i>Stomorhina lunata</i>	2
Diptera	<i>Stratiomidae sp1</i>	2
Diptera	<i>Syritta pipiens</i>	5
Diptera	<i>Syrphus ribesii</i>	4
Diptera	<i>Syrphus torvus</i>	1
Diptera	<i>Tachinidae sp1</i>	5
Diptera	<i>Tachinidae sp2</i>	4
Diptera	<i>Tachinidae sp3</i>	3
Diptera	<i>Tachinidae sp4</i>	3
Diptera	<i>Tachinidae sp5</i>	6

Order	Pollinator morphospecies	Number of contacts
Diptera	<i>Tachinidae sp6</i>	1
Diptera	<i>Tachinidae sp7</i>	3
Diptera	<i>Tachinidae sp8</i>	1
Diptera	<i>Tachinidae sp9</i>	4
Diptera	<i>Trichopoda pennipes</i>	14
Diptera	<i>Volucella inanis</i>	1
Rhyncota	<i>Acanthosoma sp1</i>	1
Rhyncota	<i>Alydidae sp1</i>	1
Rhyncota	<i>Berytidae sp1</i>	1
Rhyncota	<i>Berytidae sp2</i>	1
Rhyncota	<i>Carpocoris sp1</i>	1
Rhyncota	<i>Miridae sp1</i>	5
Rhyncota	<i>Nabidae sp1</i>	3
Rhyncota	<i>Nabidae sp2</i>	1
Rhyncota	<i>Nysius sp1</i>	6
Rhyncota	<i>Pentatomidae sp</i>	1
Rhyncota	<i>Rhopalidae sp1</i>	1
Rhyncota	<i>Stictopleurus sp1</i>	4
Hymenoptera	<i>Andrena anthrisci</i>	6
Hymenoptera	<i>Andrena coitana</i>	4
Hymenoptera	<i>Andrena falsifica</i>	2
Hymenoptera	<i>Andrena flavipes</i>	2
Hymenoptera	<i>Andrena haemorrhoa</i>	6
Hymenoptera	<i>Andrena humilis</i>	11
Hymenoptera	<i>Andrena lapida</i>	1
Hymenoptera	<i>Andrena minutula</i>	2
Hymenoptera	<i>Andrena nana</i>	1
Hymenoptera	<i>Andrena nanula</i>	6
Hymenoptera	<i>Andrena niveata</i>	3
Hymenoptera	<i>Andrena polita</i>	2
Hymenoptera	<i>Andrena sp1</i>	2
Hymenoptera	<i>Andrena sp2</i>	1
Hymenoptera	<i>Andrena tarsata</i>	2
Hymenoptera	<i>Andrena thoracica</i>	1
Hymenoptera	<i>Andrena viridescens</i>	13
Hymenoptera	<i>Andrena wilkella</i>	1
Hymenoptera	<i>Anthidium florentinum</i>	1
Hymenoptera	<i>Anthidium manicatum</i>	15
Hymenoptera	<i>Anthidium oblongatum</i>	7
Hymenoptera	<i>Anthidium septemdentatum</i>	1
Hymenoptera	<i>Apis mellifera</i>	490
Hymenoptera	<i>Astata sp1</i>	1
Hymenoptera	<i>Athalia cordata</i>	7
Hymenoptera	<i>Athalia rosae</i>	1
Hymenoptera	<i>Bembix oculata</i>	1
Hymenoptera	<i>Bombus hortorum</i>	26
Hymenoptera	<i>Bombus muscorum</i>	4
Hymenoptera	<i>Bombus pascuorum</i>	234

Order	Pollinator morphospecies	Number of contacts
Hymenoptera	<i>Bombus ruderatus</i>	1
Hymenoptera	<i>Bombus terrestris</i>	51
Hymenoptera	<i>Braconidae sp1</i>	1
Hymenoptera	<i>Cephus spinipes</i>	1
Hymenoptera	<i>Ceratina chalybea</i>	5
Hymenoptera	<i>Ceratina cucurbitina</i>	25
Hymenoptera	<i>Ceratina cyanea</i>	11
Hymenoptera	<i>Cerceris arenaria</i>	1
Hymenoptera	<i>Cerceris hortivaga</i>	3
Hymenoptera	<i>Cerceris quinquefasciata</i>	2
Hymenoptera	<i>Cerceris rybyensis</i>	5
Hymenoptera	<i>Cerceris sabulosa</i>	4
Hymenoptera	<i>Chrysis sp1</i>	5
Hymenoptera	<i>Chrysis sp2</i>	1
Hymenoptera	<i>Corynis crassicornis</i>	1
Hymenoptera	<i>Crabronidae sp1</i>	3
Hymenoptera	<i>Crabronidae sp2</i>	1
Hymenoptera	<i>Crabronidae sp3</i>	1
Hymenoptera	<i>Crabronidae sp4</i>	2
Hymenoptera	<i>Crabronidae sp5</i>	1
Hymenoptera	<i>Eucera longicornis</i>	2
Hymenoptera	<i>Eumenes coarctatus</i>	1
Hymenoptera	<i>Eumenes mediterraneus</i>	2
Hymenoptera	<i>Formicidae sp1</i>	62
Hymenoptera	<i>Gasterruptidae sp1</i>	3
Hymenoptera	<i>Halictus eurygnathus</i>	13
Hymenoptera	<i>Halictus longobardicus</i>	1
Hymenoptera	<i>Halictus maculatus</i>	3
Hymenoptera	<i>Halictus quadricinctus</i>	1
Hymenoptera	<i>Halictus rubicundus</i>	8
Hymenoptera	<i>Halictus scabiosae</i>	30
Hymenoptera	<i>Halictus subauratus</i>	11
Hymenoptera	<i>Halictus tumulorum</i>	2
Hymenoptera	<i>Heriades rubicola</i>	7
Hymenoptera	<i>Heriades truncorum</i>	11
Hymenoptera	<i>Hylaeus brevicornis</i>	1
Hymenoptera	<i>Hylaeus confusus</i>	1
Hymenoptera	<i>Hylaeus dilatatus</i>	2
Hymenoptera	<i>Hylaeus duckei</i>	1
Hymenoptera	<i>Hylaeus incongruus</i>	2
Hymenoptera	<i>Hylaeus pectoralis</i>	1
Hymenoptera	<i>Hylaeus punctatissimum</i>	1
Hymenoptera	<i>Hylaeus punctatus</i>	1
Hymenoptera	<i>Ichneumonidae sp1</i>	1
Hymenoptera	<i>Ichneumonidae sp2</i>	1
Hymenoptera	<i>Ichneumonidae sp3</i>	2
Hymenoptera	<i>Lasioglossum albipes</i>	2
Hymenoptera	<i>Lasioglossum calceatum</i>	12

Order	Pollinator morphospecies	Number of contacts
Hymenoptera	<i>Lasioglossum convexiusculum</i>	9
Hymenoptera	<i>Lasioglossum costulatum</i>	1
Hymenoptera	<i>Lasioglossum discum</i>	3
Hymenoptera	<i>Lasioglossum fulvicorne</i>	2
Hymenoptera	<i>Lasioglossum glabriusculum</i>	2
Hymenoptera	<i>Lasioglossum laevigatum</i>	5
Hymenoptera	<i>Lasioglossum laterale</i>	1
Hymenoptera	<i>Lasioglossum lativentre</i>	4
Hymenoptera	<i>Lasioglossum leucopus</i>	1
Hymenoptera	<i>Lasioglossum leucozonium</i>	4
Hymenoptera	<i>Lasioglossum limbellum</i>	1
Hymenoptera	<i>Lasioglossum malachurum</i>	1
Hymenoptera	<i>Lasioglossum marginatum</i>	21
Hymenoptera	<i>Lasioglossum morio</i>	2
Hymenoptera	<i>Lasioglossum pauxillum</i>	2
Hymenoptera	<i>Lasioglossum puncticolle</i>	28
Hymenoptera	<i>Lasioglossum pygmaeum</i>	3
Hymenoptera	<i>Lasioglossum rufitarse</i>	2
Hymenoptera	<i>Lasioglossum semilucens</i>	10
Hymenoptera	<i>Lasioglossum sexnotatum</i>	1
Hymenoptera	<i>Lasioglossum sp1</i>	4
Hymenoptera	<i>Lasioglossum sp2</i>	3
Hymenoptera	<i>Lasioglossum xanthopus</i>	1
Hymenoptera	<i>Lestica clypeata</i>	4
Hymenoptera	<i>Megachile ericetorum</i>	5
Hymenoptera	<i>Megachile leachella</i>	1
Hymenoptera	<i>Megachile pilides</i>	1
Hymenoptera	<i>Nomada argentata</i>	2
Hymenoptera	<i>Nomada facilis</i>	1
Hymenoptera	<i>Nomada sheppardana</i>	1
Hymenoptera	<i>Nomiapis diversipes</i>	8
Hymenoptera	<i>Osmia aurulenta</i>	6
Hymenoptera	<i>Osmia bicolor</i>	1
Hymenoptera	<i>Osmia rufohirta</i>	1
Hymenoptera	<i>Osmia tridentata</i>	1
Hymenoptera	<i>Polistes dominula</i>	1
Hymenoptera	<i>Priocnemis sp1</i>	1
Hymenoptera	<i>Pteromalidae sp1</i>	1
Hymenoptera	<i>Sphecodes sp1</i>	2
Hymenoptera	<i>Sphecodes sp2</i>	3
Hymenoptera	<i>Stelis phaeoptera</i>	11
Lepidoptera	<i>Adelidae sp1</i>	11
Lepidoptera	<i>Aricia agestis</i>	4
Lepidoptera	<i>Autographa gamma</i>	5
Lepidoptera	<i>Cacyreus marshalli</i>	2
Lepidoptera	<i>Coenonympha pamphilus</i>	11
Lepidoptera	<i>Colias croceus</i>	19
Lepidoptera	<i>Euclidia glyphica</i>	1

Order	Pollinator morphospecies	Number of contacts
Lepidoptera	<i>Helicoverpa armigera</i>	5
Lepidoptera	<i>Iphiclides podalirius</i>	1
Lepidoptera	<i>Lasiommata maera</i>	1
Lepidoptera	<i>Lasiommata megera</i>	2
Lepidoptera	<i>Leptotes pirithous</i>	1
Lepidoptera	<i>Lycaena phlaeas</i>	18
Lepidoptera	<i>Macroglossum stellatarum</i>	3
Lepidoptera	<i>Maniola jurtina</i>	4
Lepidoptera	<i>Melitaea athalia</i>	16
Lepidoptera	<i>Melitaea didyma</i>	9
Lepidoptera	<i>Melitaea phoebe</i>	17
Lepidoptera	<i>Noctuidae spl</i>	1
Lepidoptera	<i>Ochlodes sylvanus</i>	23
Lepidoptera	<i>Pieris brassicae</i>	5
Lepidoptera	<i>Pieris napi</i>	4
Lepidoptera	<i>Pieris rapae</i>	13
Lepidoptera	<i>Plebejus argus</i>	31
Lepidoptera	<i>Plebejus idas</i>	9
Lepidoptera	<i>Polyommatus icarus</i>	29
Lepidoptera	<i>Polyommatus thersites</i>	3
Lepidoptera	<i>Pontia edusa</i>	1
Lepidoptera	<i>Pyrausta spl</i>	6
Lepidoptera	<i>Pyrgus armoricanus</i>	3
Lepidoptera	<i>Pyrgus malvae</i>	1
Lepidoptera	<i>Pyrgus malvoides</i>	1
Lepidoptera	<i>Scythris spl</i>	1
Lepidoptera	<i>Tineola spl</i>	3
Lepidoptera	<i>Vanessa cardui</i>	3
Orthoptera	<i>Acrididae spl</i>	2
Orthoptera	<i>Tettigoniidae spl</i>	34

Table S3 Summary of the eight global models. Explanatory variables are Management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023). The continuous explanatory variables were scaled to mean 0 and standard deviation 1 to make slopes comparable.

	Type of model	Dependent variable	Independent variable	Random effect
Model 1	Linear mixed-effect model	Richness of Coleoptera species	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 2	Linear mixed-effect model	Number of contacts of Coleoptera	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 3	Linear mixed-effect model	Richness of Diptera species	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 4	Linear mixed-effect model	Number of contacts of Diptera	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 5	Linear mixed-effect model	Richness of Hymenoptera species	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 6	Linear mixed-effect model	Number of contacts of Hymenoptera	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 7	Linear mixed-effect model	Richness of Lepidoptera species	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity
Model 8	Linear mixed-effect model	Number of contacts of Lepidoptera	Management + sp_plants + n_visual + T + prec + Anno2023 + Management × sp_plants + Management × n_visual	Plot identity

Table S4: Results of the multi-model inference analysis testing the effects on richness of Coleoptera species of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management × sp_plants and management × n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-2.374	-0.209	1.044	-	-0.322	-	-	-	-	0.000	0.205	0.420	0.154
2	-2.336	-	1.049	-	-0.312	-	-	-	-	1.458	0.195	0.407	0.074
3	-2.376	-0.158	1.093	-0.165	-0.340	-	-	-	-0.110	1.506	0.204	0.420	0.072
4	-2.379	-0.204	1.053	-	-0.330	0.063	-	-	-	1.670	0.207	0.422	0.067
5	-2.373	-0.207	1.056	-0.025	-0.325	-	-	-	-	1.774	0.206	0.422	0.063
6	-2.362	-0.209	1.046	-	-0.325	-	-0.025	-	-	2.022	0.205	0.420	0.056
7	-2.373	-0.217	1.045	-	-0.321	-	-	0.009	-	2.028	0.206	0.421	0.056
8	-2.344	-	1.059	-	-0.322	0.074	-	-	-	2.965	0.197	0.411	0.035
9	-2.383	-0.153	1.108	-0.173	-0.351	0.075	-	-	-0.108	3.069	0.207	0.425	0.033
10	-2.374	-0.210	1.106	-0.190	-0.340	-	-	0.068	-0.135	3.099	0.208	0.426	0.033
11	-2.335	-	1.062	-0.026	-0.315	-	-	-	-	3.202	0.196	0.410	0.031
12	-2.380	-0.200	1.072	-0.036	-0.336	0.082	-	-	-	3.232	0.209	0.427	0.031
13	-2.325	-0.203	1.069	-	-0.349	0.095	-0.125	-	-	3.446	0.210	0.427	0.027
14	-2.324	-	1.051	-	-0.315	-	-0.026	-	-	3.474	0.195	0.408	0.027
15	-2.384	-0.158	1.092	-0.166	-0.338	-	0.018	-	-0.110	3.548	0.204	0.420	0.026
16	-2.378	-0.216	1.055	-	-0.329	0.064	-	0.013	-	3.693	0.208	0.424	0.024
17	-2.368	-0.208	1.056	-0.025	-0.326	-	-0.011	-	-	3.814	0.206	0.422	0.023
18	-2.373	-0.208	1.056	-0.025	-0.325	-	-	0.001	-	3.816	0.206	0.422	0.023
19	-2.362	-0.218	1.047	-	-0.325	-	-0.025	0.009	-	4.055	0.206	0.421	0.020
20	-2.346	-	1.081	-0.037	-0.329	0.094	-	-	-	4.448	0.200	0.416	0.017
21	-2.381	-0.206	1.122	-0.200	-0.351	0.076	-	0.070	-0.134	4.646	0.211	0.431	0.015
22	-2.283	-	1.076	-	-0.344	0.112	-0.143	-	-	4.654	0.202	0.417	0.015
23	-2.327	-0.199	1.088	-0.036	-0.355	0.114	-0.125	-	-	5.017	0.212	0.432	0.013
24	-2.350	-0.153	1.117	-0.169	-0.362	0.096	-0.079	-	-0.105	5.017	0.210	0.428	0.013
25	-2.383	-0.210	1.105	-0.192	-0.338	-	0.021	0.068	-0.136	5.144	0.208	0.426	0.012
26	-2.330	-	1.063	-0.026	-0.316	-	-0.011	-	-	5.237	0.196	0.410	0.011

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	Δ AICc	R ² marginal	R ² conditional	weight
27	-2.380	-0.204	1.072	-0.035	-0.336	0.082	-	0.003	-	5.280	0.209	0.427	0.011
28	-2.324	-0.216	1.071	-	-0.349	0.097	-0.127	0.015	-	5.468	0.211	0.429	0.010
29	-2.368	-0.208	1.057	-0.025	-0.326	-	-0.011	0.001	-	5.862	0.206	0.422	0.008

Table S5: Results of the multi-model inference analysis testing the effects on richness of Diptera species of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management × sp_plants and management × n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-1.293	-0.072	0.936	0.077	-	-	-	-	0.062	0.000	0.299	0.445	0.125
2	-1.287	-	0.970	-	-	-	-	-	-	0.557	0.297	0.442	0.095
3	-1.293	-0.072	0.933	0.077	-	-0.018	-	-	0.061	1.961	0.299	0.445	0.047
4	-1.293	-0.071	0.933	0.074	-0.015	-	-	-	0.061	1.964	0.299	0.445	0.047
5	-1.285	-	0.958	0.022	-	-	-	-	-	2.022	0.296	0.440	0.045
6	-1.293	-0.076	0.936	0.076	-	-	-	0.005	0.062	2.035	0.300	0.446	0.045
7	-1.294	-0.072	0.936	0.077	-	-	0.001	-	0.062	2.043	0.299	0.445	0.045
8	-1.285	-	0.959	-	-0.038	-	-	-	-	2.081	0.296	0.442	0.044
9	-1.286	-	0.967	-	-	-0.026	-	-	-	2.407	0.297	0.442	0.037
10	-1.288	-0.025	0.969	-	-	-	-	-	-	2.435	0.298	0.443	0.037
11	-1.307	-	0.967	-	-	-	0.041	-	-	2.468	0.297	0.442	0.036
12	-1.284	-	0.949	0.020	-0.033	-	-	-	-	3.674	0.295	0.440	0.020
13	-1.284	-	0.950	0.026	-	-0.038	-	-	-	3.704	0.295	0.440	0.020
14	-1.286	-0.025	0.957	0.022	-	-	-	-	-	3.906	0.297	0.441	0.018
15	-1.285	-0.061	0.970	-	-	-	-	0.037	-	3.918	0.300	0.445	0.018
16	-1.293	-0.072	0.930	0.075	-0.013	-0.016	-	-	0.060	3.950	0.299	0.445	0.017
17	-1.287	-0.025	0.958	-	-0.038	-	-	-	-	3.954	0.297	0.443	0.017
18	-1.302	-0.072	0.931	0.077	-	-0.022	0.018	-	0.061	3.990	0.299	0.445	0.017
19	-1.285	-	0.957	-	-0.036	-0.021	-	-	-	3.999	0.296	0.441	0.017
20	-1.299	-	0.956	0.021	-	-	0.028	-	-	4.001	0.295	0.440	0.017
21	-1.293	-0.076	0.933	0.077	-	-0.018	-	0.004	0.061	4.002	0.299	0.445	0.017
22	-1.293	-0.076	0.933	0.074	-0.015	-	-	0.005	0.060	4.004	0.299	0.445	0.017
23	-1.289	-0.072	0.933	0.075	-0.016	-	-0.008	-	0.061	4.008	0.299	0.445	0.017
24	-1.294	-0.076	0.936	0.076	-	-	0.002	0.005	0.061	4.083	0.300	0.446	0.016
25	-1.295	-	0.958	-	-0.036	-	0.018	-	-	4.091	0.296	0.442	0.016
26	-1.323	-	0.958	-	-	-0.042	0.073	-	-	4.126	0.296	0.441	0.016

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	ΔAICc	R ² marginal	R ² conditional	weight
27	-1.288	-0.026	0.966	-	-	-0.027	-	-	-	4.275	0.298	0.443	0.015
28	-1.308	-0.024	0.966	-	-	-	0.040	-	-	4.356	0.298	0.443	0.014
29	-1.282	-0.068	0.955	0.026	-	-	-	0.044	-	5.189	0.298	0.443	0.009
30	-1.283	-	0.944	0.023	-0.029	-0.032	-	-	-	5.458	0.294	0.439	0.008
31	-1.284	-0.061	0.959	-	-0.037	-	-	0.036	-	5.467	0.299	0.445	0.008
32	-1.317	-	0.943	0.025	-	-0.051	0.066	-	-	5.492	0.294	0.439	0.008
33	-1.285	-0.025	0.949	0.020	-0.034	-	-	-	-	5.554	0.296	0.441	0.008
34	-1.286	-0.027	0.949	0.026	-	-0.039	-	-	-	5.571	0.296	0.441	0.008
35	-1.288	-	0.949	0.019	-0.032	-	0.009	-	-	5.706	0.295	0.440	0.007
36	-1.307	-0.062	0.966	-	-	-	0.046	0.038	-	5.811	0.299	0.445	0.007
37	-1.284	-0.061	0.967	-	-	-0.023	-	0.035	-	5.817	0.299	0.445	0.007
38	-1.287	-0.026	0.956	-	-0.036	-0.022	-	-	-	5.866	0.297	0.443	0.007
39	-1.300	-0.025	0.955	0.021	-	-	0.027	-	-	5.893	0.297	0.441	0.007
40	-1.309	-	0.953	-	-0.029	-0.032	0.048	-	-	5.921	0.296	0.441	0.006
41	-1.296	-0.025	0.957	-	-0.036	-	0.017	-	-	5.972	0.297	0.443	0.006
42	-1.292	-0.075	0.931	0.075	-0.013	-0.016	-	0.004	0.060	5.996	0.299	0.445	0.006
43	-1.324	-0.026	0.957	-	-	-0.043	0.073	-	-	6.000	0.297	0.442	0.006

Table S6: Results of the multi-model inference analysis testing the effects on richness of Hymenoptera species of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management $\times$ sp_plants and management $\times$ n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management $\times$ sp_plants	management $\times$ n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-0.563	0.007	1.004	0.055	0.331	-	-	0.061	-	0.000	0.469	0.558	0.192
2	-0.556	-	1.018	-	0.318	-	-	-	-	0.845	0.470	0.559	0.126
3	-0.565	0.015	1.003	0.056	0.331	-	-	0.063	-0.011	1.973	0.469	0.558	0.072
4	-0.563	0.006	1.003	0.056	0.332	-0.009	-	0.060	-	2.002	0.469	0.558	0.071
5	-0.555	0.006	1.004	0.056	0.329	-	-0.016	0.061	-	2.016	0.469	0.558	0.070
6	-0.555	0.043	1.018	-	0.319	-	-	-	-	2.210	0.468	0.559	0.064
7	-0.557	-	1.017	-	0.320	-0.021	-	-	-	2.638	0.470	0.559	0.051
8	-0.556	-	1.020	-0.005	0.317	-	-	-	-	2.843	0.470	0.560	0.046
9	-0.552	-	1.019	-	0.317	-	-0.007	-	-	2.870	0.469	0.559	0.046
10	-0.552	0.024	1.018	-	0.320	-	-	-	0.023	3.863	0.468	0.559	0.028
11	-0.565	0.014	1.002	0.057	0.332	-0.010	-	0.063	-0.011	3.975	0.469	0.558	0.026
12	-0.556	0.015	1.004	0.057	0.329	-	-0.018	0.063	-0.012	3.987	0.469	0.558	0.026
13	-0.559	0.006	1.003	0.056	0.331	-0.007	-0.008	0.060	-	4.049	0.469	0.558	0.025
14	-0.556	0.042	1.017	-	0.321	-0.019	-	-	-	4.049	0.469	0.559	0.025
15	-0.555	0.043	1.020	-0.005	0.318	-	-	-	-	4.213	0.469	0.559	0.023
16	-0.553	0.043	1.018	-	0.319	-	-0.006	-	-	4.243	0.468	0.559	0.023
17	-0.567	-	1.016	-	0.323	-0.026	0.020	-	-	4.638	0.470	0.560	0.019
18	-0.557	-	1.018	-0.002	0.319	-0.020	-	-	-	4.667	0.470	0.560	0.019
19	-0.553	-	1.021	-0.005	0.317	-	-0.006	-	-	4.876	0.470	0.559	0.017
20	-0.553	0.024	1.017	-	0.321	-0.017	-	-	0.022	5.754	0.468	0.559	0.011
21	-0.552	0.024	1.020	-0.003	0.319	-	-	-	0.023	5.895	0.468	0.559	0.010
22	-0.551	0.024	1.019	-	0.319	-	-0.002	-	0.023	5.905	0.468	0.559	0.010

Table S7: Results of the multi-model inference analysis testing the effects on richness of Lepidoptera species of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management $\times$ sp_plants and management $\times$ n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management $\times$ sp_plants	management $\times$ n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-2.021	-0.212	0.924	-	0.927	0.137	-	-	-	0.000	0.253	0.462	0.096
2	-2.168	-0.204	0.913	-	0.976	-	0.264	-	-	0.180	0.262	0.473	0.088
3	-2.016	-0.212	0.915	-	0.929	-	-	-	-	0.326	0.250	0.457	0.082
4	-2.022	-0.218	0.955	-0.083	0.909	0.155	-	-	-	0.571	0.254	0.463	0.072
5	-2.177	-0.208	0.940	-0.074	0.963	-	0.281	-	-	1.054	0.262	0.474	0.057
6	-2.119	-0.208	0.920	-	0.957	0.097	0.174	-	-	1.285	0.260	0.471	0.050
7	-2.015	-0.216	0.938	-0.064	0.916	-	-	-	-	1.475	0.250	0.457	0.046
8	-2.020	-0.233	0.936	-	0.925	0.139	-	0.040	-	1.809	0.257	0.466	0.039
9	-2.122	-0.213	0.952	-0.085	0.939	0.115	0.179	-	-	1.824	0.260	0.471	0.039
10	-2.174	-0.227	0.927	-	0.976	-	0.274	0.047	-	1.910	0.266	0.479	0.037
11	-2.016	-0.228	0.925	-	0.928	-	-	0.033	-	2.202	0.253	0.461	0.032
12	-2.167	-	0.929	-	0.967	-	0.279	-	-	2.389	0.251	0.457	0.029
13	-2.021	-0.231	0.962	-0.080	0.908	0.156	-	0.027	-	2.518	0.256	0.466	0.027
14	-2.009	-	0.940	-	0.914	0.134	-	-	-	2.566	0.240	0.442	0.027
15	-2.022	-0.217	0.957	-0.093	0.908	0.155	-	-	-0.007	2.614	0.254	0.463	0.026
16	-2.004	-	0.931	-	0.918	-	-	-	-	2.817	0.237	0.438	0.023
17	-2.181	-0.225	0.948	-0.070	0.963	-	0.288	0.035	-	2.930	0.265	0.478	0.022
18	-2.125	-0.231	0.933	-	0.958	0.097	0.185	0.048	-	3.012	0.264	0.477	0.021
19	-2.180	-0.206	0.946	-0.110	0.959	-	0.285	-	-0.027	3.038	0.262	0.474	0.021
20	-2.009	-	0.969	-0.075	0.896	0.150	-	-	-	3.402	0.239	0.441	0.018
21	-2.015	-0.227	0.943	-0.061	0.915	-	-	0.023	-	3.446	0.251	0.459	0.017
22	-2.174	-	0.953	-0.068	0.954	-	0.295	-	-	3.455	0.251	0.457	0.017
23	-2.016	-0.215	0.940	-0.080	0.914	-	-	-	-0.012	3.504	0.249	0.456	0.017
24	-2.122	-	0.935	-	0.949	0.089	0.197	-	-	3.636	0.248	0.453	0.016
25	-2.126	-0.229	0.960	-0.081	0.940	0.114	0.186	0.034	-	3.717	0.263	0.475	0.015
26	-2.125	-0.211	0.955	-0.109	0.937	0.113	0.182	-	-0.018	3.849	0.260	0.471	0.014

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	ΔAICc	R ² marginal	R ² conditional	weight
27	-2.002	-	0.952	-0.057	0.905	-	-	-	-	4.147	0.236	0.437	0.012
28	-2.123	-	0.964	-0.077	0.932	0.104	0.201	-	-	4.433	0.248	0.453	0.010
29	-2.022	-0.233	0.970	-0.114	0.904	0.156	-	0.035	-0.026	4.524	0.256	0.466	0.010
30	-2.189	-0.230	0.966	-0.146	0.956	-	0.300	0.054	-0.059	4.755	0.267	0.480	0.009
31	-2.016	-0.229	0.952	-0.098	0.911	-	-	0.032	-0.029	5.433	0.252	0.460	0.006
32	-2.134	-0.233	0.973	-0.141	0.935	0.110	0.199	0.049	-0.047	5.633	0.264	0.477	0.006

Table S8: Results of the multi-model inference analysis testing the effects on number of contacts of Coleoptera of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management × sp_plants and management × n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-2.212	-	1.327	-	-0.354	-	-	-	-	0.000	0.244	0.463	0.171
2	-2.095	-	1.347	-	-0.390	-	-0.275	-	-	0.675	0.249	0.470	0.122
3	-2.218	-	1.317	-	-0.354	-0.093	-	-	-	1.330	0.244	0.464	0.088
4	-2.213	-	1.346	-0.041	-0.359	-	-	-	-	1.705	0.245	0.466	0.073
5	-2.213	-0.053	1.322	-	-0.352	-	-	-	-	1.882	0.244	0.462	0.067
6	-2.092	-0.073	1.342	-	-0.389	-	-0.291	-	-	2.433	0.250	0.469	0.051
7	-2.101	-	1.361	-0.031	-0.392	-	-0.262	-	-	2.532	0.250	0.472	0.048
8	-2.110	-	1.342	-	-0.386	-0.025	-0.243	-	-	2.681	0.249	0.469	0.045
9	-2.235	-0.024	1.395	-0.233	-0.380	-	-	-	-0.158	3.081	0.248	0.469	0.037
10	-2.221	-0.074	1.309	-	-0.351	-0.104	-	-	-	3.082	0.244	0.463	0.037
11	-2.218	-	1.333	-0.031	-0.358	-0.085	-	-	-	3.184	0.246	0.466	0.035
12	-2.214	-0.053	1.341	-0.042	-0.356	-	-	-	-	3.589	0.245	0.465	0.028
13	-2.212	-0.055	1.322	-	-0.352	-	-	0.005	-	3.918	0.244	0.462	0.024
14	-2.136	-0.041	1.400	-0.204	-0.405	-	-0.226	-	-0.143	4.269	0.251	0.473	0.020
15	-2.098	-0.072	1.355	-0.031	-0.391	-	-0.278	-	-	4.300	0.251	0.471	0.020
16	-2.112	-0.077	1.334	-	-0.383	-0.035	-0.248	-	-	4.415	0.249	0.468	0.019
17	-2.087	-0.083	1.344	-	-0.390	-	-0.295	0.021	-	4.451	0.250	0.470	0.018
18	-2.240	-0.043	1.377	-0.219	-0.378	-0.093	-	-	-0.156	4.478	0.248	0.468	0.018
19	-2.111	-	1.357	-0.030	-0.389	-0.018	-0.240	-	-	4.559	0.250	0.471	0.017
20	-2.223	-0.059	1.409	-0.264	-0.383	-	-	0.092	-0.191	4.718	0.249	0.471	0.016
21	-2.221	-0.073	1.325	-0.030	-0.355	-0.095	-	-	-	4.952	0.246	0.465	0.014
22	-2.220	-0.077	1.310	-	-0.351	-0.104	-	0.007	-	5.122	0.245	0.463	0.013
23	-2.216	-0.050	1.341	-0.043	-0.356	-	-	-0.008	-	5.627	0.245	0.465	0.010
24	-2.119	-0.081	1.416	-0.235	-0.410	-	-0.237	0.100	-0.178	5.832	0.253	0.475	0.009

Table S9: Results of the multi-model inference analysis testing the effects on number of contacts of Diptera of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management × sp_plants and

management $\times$ n_visual. The table reports the estimates for each variable, the ΔAICc , the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta\text{AICc} < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management $\times$ sp_plants	management $\times$ n_visual	ΔAICc	R^2 marginal	R^2 conditional	weight
1	-1.127	0.011	1.136	0.092	-	0.118	-	-	0.084	0.000	0.366	0.526	0.076
2	-1.116	0.019	1.112	0.097	-	-	-	-	0.076	0.717	0.359	0.518	0.053
3	-1.112	-	1.108	0.102	-	-	-	-	-	0.901	0.361	0.521	0.049
4	-1.120	-	1.129	0.099	-	0.100	-	-	-	0.911	0.368	0.528	0.048
5	-1.126	0.013	1.128	0.083	-0.050	0.123	-	-	0.081	1.483	0.366	0.526	0.036
6	-1.123	-0.007	1.139	0.090	-	0.116	-	0.031	0.078	1.863	0.367	0.527	0.030
7	-1.181	0.020	1.105	0.089	-	-	0.128	-	0.074	1.911	0.359	0.518	0.029
8	-1.146	0.011	1.132	0.090	-	0.109	0.039	-	0.083	1.983	0.365	0.525	0.028
9	-1.179	-	1.101	0.092	-	-	0.131	-	-	2.043	0.361	0.521	0.027
10	-1.120	-	1.119	0.087	-0.057	0.106	-	-	-	2.218	0.367	0.528	0.025
11	-1.125	-	1.182	-	-	0.106	-	-	-	2.318	0.371	0.530	0.024
12	-1.115	0.052	1.118	0.095	-	-	-	-	-	2.424	0.362	0.521	0.023
13	-1.115	0.021	1.105	0.090	-0.038	-	-	-	0.073	2.429	0.358	0.518	0.023
14	-1.111	-	1.099	0.092	-0.045	-	-	-	-	2.454	0.360	0.520	0.022
15	-1.112	-0.001	1.115	0.094	-	-	-	0.036	0.069	2.511	0.359	0.519	0.022
16	-1.122	0.047	1.137	0.093	-	0.098	-	-	-	2.523	0.368	0.528	0.022
17	-1.116	-	1.161	-	-	-	-	-	-	2.607	0.364	0.523	0.021
18	-1.124	-	1.158	-	-0.082	0.115	-	-	-	2.748	0.370	0.530	0.019
19	-1.150	-	1.123	0.095	-	0.087	0.060	-	-	2.794	0.367	0.527	0.019
20	-1.205	-	1.145	-	-	-	0.175	-	-	2.981	0.364	0.524	0.017
21	-1.104	0.002	1.123	0.090	-	-	-	0.077	-	3.167	0.362	0.522	0.016
22	-1.112	-0.002	1.142	0.087	-	0.098	-	0.077	-	3.264	0.368	0.529	0.015
23	-1.122	-0.006	1.131	0.081	-0.052	0.122	-	0.035	0.074	3.305	0.367	0.527	0.015
24	-1.113	-	1.139	-	-0.071	-	-	-	-	3.397	0.363	0.522	0.014
25	-1.128	0.069	1.188	-	-	0.103	-	-	-	3.451	0.371	0.530	0.014
26	-1.130	0.013	1.127	0.083	-0.049	0.121	0.007	-	0.081	3.534	0.366	0.526	0.013
27	-1.182	0.053	1.111	0.085	-	-	0.132	-	-	3.556	0.362	0.521	0.013
28	-1.120	0.074	1.170	-	-	-	-	-	-	3.604	0.365	0.524	0.013
29	-1.179	-0.003	1.108	0.085	-	-	0.135	0.042	0.065	3.622	0.360	0.520	0.012

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	ΔAICc	R ² marginal	R ² conditional	weight
30	-1.122	0.050	1.128	0.080	-0.058	0.105	-	-	-	3.791	0.367	0.528	0.011
31	-1.175	0.021	1.100	0.085	-0.026	-	0.116	-	0.072	3.806	0.358	0.518	0.011
32	-1.170	-	1.095	0.086	-0.034	-	0.116	-	-	3.819	0.361	0.520	0.011
33	-1.145	-0.007	1.134	0.087	-	0.106	0.047	0.033	0.076	3.824	0.366	0.526	0.011
34	-1.178	-	1.167	-	-	0.083	0.108	-	-	3.830	0.369	0.529	0.011
35	-1.126	0.068	1.166	-	-0.081	0.112	-	-	-	3.901	0.370	0.530	0.011
36	-1.114	0.054	1.109	0.085	-0.047	-	-	-	-	3.944	0.361	0.521	0.011
37	-1.117	0.013	1.192	-	-	0.104	-	0.083	-	3.969	0.372	0.532	0.010
38	-1.207	0.071	1.153	-	-	-	0.172	-	-	4.045	0.365	0.524	0.010
39	-1.177	0.000	1.115	0.079	-	-	0.145	0.082	-	4.118	0.362	0.523	0.010
40	-1.108	0.019	1.173	-	-	-	-	0.081	-	4.177	0.366	0.525	0.009
41	-1.110	-0.001	1.108	0.087	-0.040	-	-	0.039	0.065	4.183	0.359	0.519	0.009
42	-1.132	-	1.117	0.086	-0.054	0.101	0.026	-	-	4.234	0.367	0.527	0.009
43	-1.189	-	1.130	-	-0.055	-	0.148	-	-	4.319	0.363	0.522	0.009
44	-1.115	0.010	1.169	-	-0.084	0.113	-	0.086	-	4.323	0.371	0.532	0.009
45	-1.153	0.048	1.131	0.088	-	0.085	0.063	-	-	4.394	0.367	0.527	0.008
46	-1.201	0.013	1.156	-	-	-	0.184	0.087	-	4.400	0.366	0.526	0.008
47	-1.117	0.072	1.148	-	-0.071	-	-	-	-	4.417	0.363	0.523	0.008
48	-1.111	-0.002	1.133	0.074	-0.062	0.105	-	0.080	-	4.435	0.368	0.529	0.008
49	-1.102	0.002	1.113	0.080	-0.051	-	-	0.079	-	4.608	0.362	0.522	0.008
50	-1.150	-	1.153	-	-0.075	0.102	0.055	-	-	4.661	0.369	0.529	0.007
51	-1.105	0.016	1.151	-	-0.073	-	-	0.084	-	4.901	0.364	0.525	0.007
52	-1.180	0.068	1.174	-	-	0.081	0.107	-	-	4.976	0.369	0.528	0.006
53	-1.150	-0.003	1.135	0.081	-	0.081	0.079	0.080	-	5.048	0.367	0.528	0.006
54	-1.173	0.054	1.105	0.079	-0.036	-	0.117	-	-	5.308	0.361	0.521	0.005
55	-1.129	-0.006	1.129	0.080	-0.050	0.118	0.015	0.035	0.073	5.356	0.366	0.527	0.005
56	-1.175	0.011	1.176	-	-	0.079	0.120	0.086	-	5.375	0.370	0.530	0.005
57	-1.191	0.071	1.139	-	-0.055	-	0.145	-	-	5.385	0.363	0.523	0.005
58	-1.172	-0.003	1.103	0.081	-0.029	-	0.122	0.044	0.063	5.494	0.359	0.520	0.005
59	-1.184	0.012	1.142	-	-0.057	-	0.156	0.088	-	5.705	0.364	0.525	0.004
60	-1.136	0.050	1.125	0.079	-0.055	0.098	0.029	-	-	5.806	0.367	0.527	0.004
61	-1.153	0.067	1.160	-	-0.074	0.100	0.055	-	-	5.821	0.369	0.529	0.004

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management×sp_plants	management×n_visual	Δ AICc	R ² marginal	R ² conditional	weight
62	-1.168	0.000	1.109	0.072	-0.039	-	0.129	0.084	-	5.829	0.362	0.522	0.004

Table S10: Results of the multi-model inference analysis testing the effects on number of contacts of Hymenoptera of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management $\times$ sp_plants and management $\times$ n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management $\times$ sp_plants	management $\times$ n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-0.197	-	1.204	-	0.583	0.151	-0.461	-	-	0.000	0.397	0.527	0.314
2	-0.202	-	1.226	-0.062	0.575	0.156	-0.453	-	-	1.172	0.397	0.528	0.174
3	-0.197	0.020	1.204	-	0.584	0.151	-0.461	-	-	1.980	0.396	0.527	0.117
4	-0.274	-	1.189	-	0.586	-	-0.294	-	-	2.206	0.393	0.523	0.104
5	-0.202	0.020	1.227	-0.062	0.576	0.157	-0.453	-	-	3.159	0.397	0.528	0.065
6	-0.280	-	1.207	-0.050	0.579	-	-0.282	-	-	3.650	0.393	0.524	0.051
7	-0.194	0.013	1.209	-	0.582	0.152	-0.461	0.025	-	3.914	0.397	0.528	0.044
8	-0.274	0.016	1.189	-	0.586	-	-0.293	-	-	4.203	0.392	0.522	0.038
9	-0.212	0.029	1.241	-0.127	0.571	0.151	-0.438	-	-0.058	4.530	0.398	0.530	0.033
10	-0.199	0.014	1.230	-0.060	0.575	0.157	-0.453	0.019	-	5.142	0.397	0.529	0.024
11	-0.281	0.015	1.208	-0.050	0.579	-	-0.281	-	-	5.656	0.393	0.523	0.019
12	-0.415	-	1.163	-	0.587	-	-	-	-	5.657	0.387	0.517	0.019

Table S11: Results of the multi-model inference analysis testing the effects on number of contacts of Lepidoptera of management, plant species richness (sp_plant), number of floral visual displays (n_visual), temperature (T), precipitation (prec), year (Anno2023).and the following interactions: management $\times$ sp_plants and management $\times$ n_visual. The table reports the estimates for each variable, the $\Delta AICc$, the marginal R^2 , the conditional R^2 and the Akaike weight for each model with $\Delta AICc < 6$. All the explanatory variables were scaled to mean 0 and standard deviation 1.

Ranking	Intercept	management	sp_plants	n_visual	T	prec	Anno2023	management $\times$ sp_plants	management $\times$ n_visual	$\Delta AICc$	R^2 marginal	R^2 conditional	weight
1	-1.936	-0.318	1.025	0.356	1.136	0.196	-	-	0.313	0.000	0.315	0.555	0.329
2	-1.927	-0.298	0.997	0.363	1.150	-	-	-	0.299	1.397	0.308	0.546	0.164
3	-1.986	-0.316	1.024	0.353	1.151	0.180	0.087	-	0.311	1.895	0.318	0.558	0.128
4	-1.941	-0.305	1.014	0.360	1.143	0.197	-	-0.043	0.321	1.904	0.314	0.553	0.127
5	-2.055	-0.298	1.002	0.355	1.185	-	0.215	-	0.298	2.323	0.317	0.556	0.103
6	-1.932	-0.287	0.989	0.366	1.156	-	-	-0.039	0.307	3.323	0.307	0.544	0.062
7	-1.988	-0.305	1.014	0.357	1.157	0.181	0.082	-0.040	0.319	3.825	0.316	0.556	0.049
8	-2.056	-0.289	0.995	0.358	1.190	-	0.212	-0.032	0.304	4.294	0.316	0.554	0.038

Conclusions

This doctoral thesis explored the role and various approaches to implementing ecological intensification in intensive agricultural landscapes. Each chapter investigated strategy for restoring and managing semi-natural habitats and their effects on different plant and beneficial arthropod communities. The results showed that the restoration and proper management of semi-natural habitats can support agricultural biodiversity and favour both pollinators and natural enemies.

Overall, results revealed the fundamental role of plant community composition and structure in shaping arthropod communities, as well as their functional and trophic groups. The availability of floral resources (e.g. nectar, pollen), along with plant species richness, structural attributes of the plant community (e.g., cover, height), and plant functional traits should be carefully considered in the design and management of semi-natural habitats. Furthermore, our study underlined the importance of considering the relationship between restored areas and the local and landscape contexts in which semi-natural habitats are established. Our results demonstrated that habitat restoration and enhancement practices can have different effects depending on spatial scale and the specific pollinator community considered. Finally, the management of semi-natural habitats play a crucial role in supporting the different pollinator communities. Extensive and semi-abandoned management hay meadows have demonstrated their importance in supporting agricultural biodiversity of pollinators, specifically lepidopterans, which rely not only on available floral resources but also on host plants. Therefore, habitat management serve as a valuable tool for enhancing the adaptability of plant and pollinator communities.

Despite these promising results, which provide useful insights to guide the design and management of semi-natural habitats, several questions and challenges remain unresolved. For example, further research is needed to assess the long-term stability and effectiveness of restored and improved habitats, their ability to consistently reduce crop damage, and the long-term dynamics of the arthropod communities they support. In addition, finding a balance between promoting pollinators and natural enemies in semi-natural habitat restoration and management remains an open question, as potential and unintended trade-offs between these two ecological functions are still poorly understudied.

In conclusion, the research provided empirical evidence supporting the role of ecological intensification practices in fostering a more sustainable agricultural system. By integrating ecological restoration with biodiversity-friendly agricultural practices, pollinator and natural enemy communities can be enhanced, potentially improving pollinator and pest control ecosystem services. Ultimately, these approaches may contribute to the development of more resilient agricultural systems, advancing the transition toward sustainable and environmentally responsible food production.