Impact of landscape characteristics on flower-visiting insects in agricultural environments across Europe

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Declaration

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Irene Bottero –

Summary

In the last few decades, there has been growing concern about the decline in insect communities in Europe, including pollinators. One-third of syrphids and butterflies are considered to be in decline, and nearly one out of ten species of wild bees are threatened with extinction. Because flower-visiting insects provide a pollination service, declines might have consequences for ecosystems, human health and food production. One of the major drivers of insect decline is habitat loss, fragmentation and degradation. However, the responses of insects to different landscape composition and configuration heterogeneity vary, depending on their taxa and their ecological requirements, as well as according to the spatial and temporal scales considered. Data collection with standard methods on a wide geographic range can promote deeper knowledge of the current status of insects in Europe and their responses to landscape context, and enables comparisons across regions characterised by different environments. However, the use of standardised methods to study the impact of landscape composition and configuration across different biogeographic ranges is rare.

It is in this context that my study takes place. Thanks to participation in a collaborative project (PoshBee project; Brown et al., 2021), my studies contribute knowledge, on a large-scale (across eight European countries), regarding the impacts of landscape features on five insect groups (honey bees, bumble bees, solitary bees, hover flies and butterflies), in two agricultural crops (apple and oilseed rape). Field-collected data were processed by research partners across a network of fourteen countries, covering different areas of investigation, so as to define, at a deeper level, which risks represent threats to the health of pollinators across Europe. In this thesis, my focus was gathering more data on the abundance of pollinator groups commonly present in cultivated fields in Europe and investigating whether they were threatened by landscape degradation and homogenization. I investigated the impact of the agricultural landscape and less-intensively managed/non-crop habitats on these communities, to provide data to implement or support agricultural policies already in force (Agri-Environmental Scheme – AES) and to suggest new ad hoc projects for different groups of insects in different agricultural habitats.

To investigate the impact that landscape has on the abundance of insect groups, I carried out three studies across different biogeographic areas in Europe. For the first, I used information about the composition and configuration heterogeneity of the landscape surrounding 128 sites at a 1 km radius. The sites were oilseed rape crops and apple orchards in Estonia, Spain, Germany, Great Britain, Ireland, Italy, Sweden, Switzerland (eight oilseed rape fields and eight apple orchards per country). The PoshBee team sampled the abundance of five groups of flower-visiting insects (honey bees, bumble bees, solitary bees, hover flies and butterflies) with 50 m long transects, during the flowering period of the target crops. I focussed on data collection in the 16 Irish sites. Using mixed effect models, I investigated the impact of landscape features on the abundance of each of the insects groups in the two crop types. The models included country as a random factor and some climate variables (annual temperature and precipitation and precipitation seasonality) as independent variables. Our results showed a positive impact of less-intensively managed and diverse habitats on the abundance of different groups of insects, even though the effect was taxon and crop specific.

In the second study, I focused on insect groups in oilseed rape crops and apple orchards, located into a specific agricultural context, namely intensively managed grassland in Ireland. Across eleven sites, I used 100 m long transects to sample insects present along the flowering margins and in the centre of the cultivated crops, at three different periods of the year. At the same time, I surveyed the plants present along the margins of the field, using quadrats (1 m x 1 m). My goal was to investigate differences in the insect groups between the margins and the centres of crops and whether the changes in insects and floral communities through time were related. The results of the linear models (REML) showed that some groups of insects (hover flies and butterflies) were more abundant along the margins of the crops, rather than in their centres, across all three periods. Moreover, I found that although both insects and flower communities changed through the time (REML and NMDS models), this change was not correlated, except for a moderate correlation emerging between plant diversity and bumble bee abundance.

In my third study, I investigated the role of the landscape on the fitness of *Osmia bicornis*, a solitary bee species, across Europe. Three *O. bicornis* nests were established in 96 apple and oilseed rape crops, in Estonia, Germany, Italy, Spain, Sweden, Switzerland and information on the pollen stored in the nests, and about different developmental stages of *O. bicornis* (occupation of the nests, number of pupae, number of adult hatched and their weight and sex ratio), was collected. We used the 1 km radius maps to check, with the use of mixed effect models, the impact of the non-crop landscape on the composition of the pollen (pollen from crop and non-crop species of plants, and pollen diversity) and on the occupation of the nests, in the two crops. We analysed the relationship of non-crop pollen and the different developmental stages of the bees. From this study, it emerged that there was a positive impact of the non-crop habitats on the non-crop pollen present in the nest. Moreover, we found that more adults hatched from those nests where the percentage of non-crop pollen was higher, suggesting an indirect impact of non-cultivated habitats of *O. bicornis* fitness.

Overall, my results show that, independent of the biogeographic area considered, semi-natural habitats, non-cultivated habitats and less-intensively managed habitats support a high abundance of flower visiting insects in agricultural crops, both at a crop- and at a landscape-scale. However, this effect is taxon- and crop-specific. This suggests a positive role for natural elements on biodiversity. Guaranteeing the presence of insects in cultivated crops can both support the production of the crops themselves, given the role of insects as pollinators, and increase the biodiversity of the landscape, with positive repercussion on the ecosystem and on human health.

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CHAPTER 1

General Introduction

1. GENERAL INTRODUCTION

1.1 Flower-visiting insects and their conservation in Europe

Insects have a key role in the ecosystem, providing several services, including pollination, that benefit both crop and wild plants. Globally, 60-90% of angiosperm species benefit from animal pollination for sexual reproduction (Ollerton et al. 2011). Currently, 75% of all crop species that are used directly for human food worldwide, accounting for approximately 35% of crop production, benefit from animal pollinators, with 30% of crop species highly dependent, and 27% moderately dependent (Klein et al. 2007). Animal pollination increases the quality and the quantity of food production, even for self-fertile species, such as oilseed rape, sunflowers, cotton, pepper and tomatoes (Ghazoul, 2005; Klein at al. 2006; Winfree et al. 2009; Potts, et al.,2010 a; Grünewald, 2010. In Europe, 84% of crops and nearly 80% of wild species of plants benefit from insect pollination (Potts et al., 2010 b). The global annual financial value of insect pollinators has been estimated to be around €153 billion (in Europe € 22 billion; Gallai et al., 2009; Melathopoulos et al., 2015; Ollerton et al., 2011; Potts et al., 2010 b), with recent estimates suggesting it to be even greater, taking into account trade in animal-pollinated crops (Stout et al. 2019).

Because honey bees, bumble bees, solitary bees, hover flies and butterflies are all flower-visiting insects, they actively contribute to pollination. Specifically, bees are responsible for the pollination of 60 to 70% of all flowering plant species (Larsen et al., 2005). Honey bees (*Apis mellifera*) are relatively easy to manage, and thus widely used in cultivation, but wild bees, including bumble bees, and non-bee insects (e.g. flies, beetles, moths, butterflies, wasps, ants and hoverflies) are equally effective, or, in some cases, more efficient, pollinators (Garibaldi et al., 2013; Melathopoulos et al., 2015; Potts et al., 2010 b; Power et al., 2016; Rader et al., 2016). Besides honey bees, some bumble bees and solitary bees (e.g. *Bombus terrestris, Osmia bicornis*) are considered managed species (Osterman et al., 2021).

Despite the diet of these five taxa of insects being mainly made up of pollen and nectar, differences emerge both between and within the same group. Some of them are polylectic and feed on a wide range of plants groups, others are oligolectic (feeding on a single genus or group of plants) or even monolectic (feeding on a single plant species; Faulk & Lewinghton, 2018). Adult butterflies mainly feed on liquid substances, such as nectar, given the conformation of their mouthparts (Snodgrass, 1935; Watt et al., 1974). Adult bees also use nectar as a source of carbohydrates (Nicolson et al., 2007) and mix it with the pollen for feeding the larvae (Michener, 2007). Pollen is used by adult bees as a source of lipids and protein (Vaudo et al., 2015) and it is necessary for the development of bees larvae (Cane et al., 2011). In some groups of bees (honey bees and to a lesser extent bumble bees), nectar is also used to produce honey. Adult hover flies feed on nectar and pollen, their larvae diets vary between the taxa, with some groups having predatory larvae feeding on plant-feeding true bugs (Hemiptera), others being saprophagous or microphagous, or feeding on plant tissues (Speight et al., 2010).

Honey bees, bumble bees, solitary bees, hover flies and butterflies are holometabolous, experiencing metamorphosis during their developmental stages. The majority of bees are ground nesters, but some build their nests in holes in trees or wood (e.g. some species of solitary bees) and others live in colonies (honey bees and bumble bees; Faulk & Lewinghton, 2018). On the other hand, butterflies do not nest, but use different habitats for the different stages of their life cycle (Erhardt, 1985; Erhardt & Mevi-Schütz, 2009). Honey bees and bumble bees have an eusocial organisation and live in colonies, the hover flies, butterflies and the other bee groups generally conduct a solitary life, or are kleptoparasites, or primitively eusocial, or communal. Parasitic behaviour is also present in some bumble bee species, the so-called cuckoo bumble bees, that usurp other bumble bee species nests (Erhardt, 1985; Erhardt & Mevi-Schütz, 2009; Speight et al., 2010; Faulk & Lewinghton, 2018).

There is global concern about the risk of flower-visiting insect decline (Biesmeijer et al. 2006; Cameron et al. 2010; Zattara and Aizen, 2019), even though studies are generally geographically or taxonomically limited (Saunders et al. 2020). Different studies report a decline in the abundance and richness of several taxonomic groups across Europe (Nieto et al., 2014; Van Swaay et al., 2010; IUCN Red List, 2022). Whilst honey bee decline has been mainly observed in USA and Europe (vanEngelsdorp et al., 2008; Potts et al., 2016; FAOSTAT, 2008), a deeper concern is the decline of other groups of pollinating insects. Overall, 0.4% of European bee species are considered critically endangered, 2.4% endangered, 1.2 % vulnerable and 5.2% nearly threatened (Nieto et al., 2014). However, given a high deficiency in the data available to make assessments, the threatened species are estimated to be between 4% and 60.7% (Nieto et al., 2014). Biesmeijer et al., (2006) found a significant decline of bee diversity in Netherlands and UK, when comparing data before and after 1980. Similarly, a decline in bumble bees has been documented in Europe for the last 60 years (Goulson et al. 2008), where 23.6% of the species of bumble bees are considered threatened and 4.4% nearly threatened (Nieto et al., 2014). Non-bee groups are considered in danger as well – 37% of European hover fly species are threatened with extinction (IUCN Red List, 2022) and 1% of butterflies species are considered as critically endangered, 3% endangered, 5% vulnerable and 10% nearly threatened (Van Swaay et al., 2010). According to Warren et al. (2001), overall three-quarters of butterfly species have declined in distribution area in Britain.

Despite general declines, some groups of insects might be considered more at risk than others, given their diet requirements, mobility or ecological traits (Biesmeijer et al., 2006). The level of specialisation in the diet (a spectrum that goes from generalist to specialist) seems to be correlated with a decrease of pollinator species richness, suggesting that specialist species are the most vulnerable and most subjected to decline, compared to generalists (Potts et al., 2010 a; Potts et al., 2010 b; Warren et al., 2001). Similarly, lower mobility was correlated with higher decline, in both bee and non-bee pollinators (Warren et al. 2001; Biesmeijer et al. 2006). In addition, some phenological characteristics, such as the time of year when individuals are more active or hatch and reproduce, might make some species more vulnerable to decline – univoltine species, that only have one generation per year, are more affected by the decline in comparison with multivoltine species (Biesmeijer et al., 2006). Similarly, a study conducted in Ireland and Britain showed that within bumble bee species, those whose queens emerged later in the season were more vulnerable to decline. This was probably related to the conversion of agricultural systems from traditional hay-meadows to a system based on silage, which results in earlier and more frequent mowing, causing consequent nutritional gaps in the late summer (Fitzpatrick et al., 2007).

Considering the role of pollinators as ecosystem service providers, their worldwide decline can have consequences on a wider scale, with a cascade effect on the entire ecosystem and on the biodiversity of numerous groups of plants, and with repercussion of plant-pollinator networks.

1.2 Threats contributing to flower-visiting insects decline

The main factors contributing to flower-visiting insects decline are attributed to anthropogenic activity. This is connected with the degradation of landscapes and habitats (e.g. homogenisation of the landscape, habitat loss, fragmentation and isolation, conversion of semi-natural habitats into intensively managed cultures and monoculture), with the use of pesticides, with the introduction of alien species, including pests and diseases, and phenomena related to climate change (Potts et al., 2010 a; Goulson et al., 2015).

1.2.1 Pesticides

Agrochemicals products include fungicides, herbicides and insecticides (known collectively as pesticides or plant protection products – PPP), as well as fertilizers. Such chemicals are used in agriculture to support crop production to eradicate plants and pests that can damage the crop, or to improve crop plant growth. Pesticides can be sprayed directly on the target crop whilst growing, or used to dress their seeds before planting. Once applied on the plants, pesticides might translocate within plant tissues or some droplets might run along the outside tissues to other parts of the plant. Zioga et al. (2020) in their review, identified 31 fungicides and insecticides that have been found as residues in the pollen and nectar of plants. Similarly, pesticides can spread in the ecosystem, where they can persist for long periods, contaminating soil, air and surface and groundwater resources (Sur and Stork 2003; Arias-Estevez et al. 2008; Samson-Robert et al. 2014; Wood and Goulson, 2017; Casado et al., 2019; Silva et al., 2019). Given their presence in the environment and in different tissues of plants, non-target animals, including flower-visiting insects, can be exposed to a mixture of toxic residues (Botías et al., 2016; Gavrilescu, 2005; Looser et al., 2000). The exposure can happen through direct contamination (particles in the air) when these products are applied in the fields, or through contact with contaminated substrates (pollen, nectar, soil, plant surfaces; Greig-Smith et al., 1994; Pistorius et al., 2015; Bonmatin et al., 2015; Boyle et al., 2019). The negative impact of pesticides on different groups of insects is supported by evidence (Goulson et al. 2015; Sànchez-Bayo, 2021). Insecticides are the most studied, but there is increasing evidence that other pesticides that target plants and fungi can, on their own or in combination with other chemicals, have a negative impact on insects as well (Tosi et al., 2022). Both contact and oral exposure poses high risk to insects, causing a direct increase in mortality (Alston et al., 2007), or a decrease in reproductive fitness, as a result of the modification of some behaviours (e.g. mating, flight, learning and spatial memory), or of some physiological characteristics of the organisms such as lower immune-responses, damage to the reproductive system) (Potts et al., 2010 a; Goulson et al., 2015). Moreover, additional risk is represented by herbicides that reduce the abundance and the diversity of floral resources (Sànchez-Bayo, 2021). For these reasons, bee and plant abundance and species richness were found to decrease linearly with the increasing use of pesticides in farmland (Kovács-Hostyánszki et al., 2011), even after one year following pesticide exposure (Park et al., 2015). However, the risk associated with the use of pesticides varies between species and sexes, and it depends on the type of ingredients the organisms are exposed to, as well as on their concentration in the products and on whether such products are applied alone or in combination with others (Spurgeon, 2016; Brandt et al., 2020; Linguadoca et., 2022; Mokkapati, 2022).

1.2.2 Climate change

The effects of extreme weather events correlated with climate change (such as droughts and flooding, fires and storms) can, directly or indirectly, impact insect communities (Potts et al., 2010 a; Goulson et al., 2015). Climate change has been connected to a change in butterfly distribution (Hickling et al., 2006; Potts et al., 2010 a) and similar effects are predicted for bees (Williams & Osborne, 2009; Goulson et al., 2015). High temperatures cause weight loss amongst some species of bees (with repercussion for the fitness of the population itself; Radmacher, & Strohm, 2010). Climate change can also impact the phenology and behaviour of insects, with ramifications for their life cycle, including a mismatch with flower blossoming (Hegland et al., 2009), changes in physiological traits, e.g. the prolongation of breeding season (Grünewald et al. 2010), or migration to more suitable areas (Hegland et al., 2009; Grünewald et al. 2010; Soroye et al. 2020). For example, arid habitats could induce bees to migrate towards more humid regions and changes in temperature might cause the colonisation of formerly cold areas that are becoming warmer (Grünewald et al. 2010; Soroye et al. 2020). In this context, a recent study by Soroye et al. (2020), tried to predict the changes in bumble bee species richness in Europe and USA, depending on the colonisation and extinction dynamics. According to their predictive model, the probability of site occupancy by bumble bee species declined when the temperatures exceeded species' thermal tolerance, and increased with heating of regions with historical temperatures close to a species' cold limit. Moreover, the occupancy of sites decreased with increasing drought. Overall, the rate of extirpation related to climate change was greater than the colonisation rate, driving bumble bee species decline in both the USA and Europe (Soroye et al. 2020).

The intensification of some weather phenomena correlated to climate change can impact habitat availability, and floral abundance and richness, making it more difficult for insects to find nesting and food resources. Similarly, a shift in floral and/or insect phenology, related to increased temperatures, has been documented. This can cause divergences in temporal and spatial co-occurrence between insects and those plants that depend on them for pollination, resulting in a potential disruption of their interactions (Goulson et al., 2015; Potts et al., 2010 a). Alteration in the distribution of flowers could help the proliferation of alien species with negative consequences on the native species (Schweiger et al., 2010). Moreover, weather events can limit the food availability in other ways, such as limiting pollen and nectar availability. Strong rainfall might wash away pollen from flowers or dilute the nectar (Lawson and Rands, 2019), while arid periods might prevent sufficient nectar flow or pollen production (Grünewald et al. 2010).

Nevertheless, the consequences of climate change for insects are not homogeneous (Kiritani, 2013). Different species respond in different ways to climate change and the intensity of the effects might depend on the geographic context.

1.2.3 Alien and invasive species, including pests and diseases

Alien species are defined as non-native species that are accidentally or intentionally introduced in a new environment by humans. In the new habitats, alien species might become invasive, spreading rapidly and becoming ecologically dominant. This can have consequences for the local ecosystem, affecting its functioning and its composition and impacting native species. The effects that invasive pollinator species can have on local insects and plant populations are both direct – predation, physical impact, hybridisation – or indirect – nest or other resource competition, or alteration of resources (Frenkie et al. 1998; Stout and Morales, 2009).

In addition, the introduction of alien species can also impact plant communities with cascade effects on plant-pollinator networks. Alien insects might promote the pollination of non-native species at the expense of native ones (Stout and Morales, 2009), while the competition for resources of alien plants with the native plants can decrease the floral diversity and abundance (Tiedeken and Stout, 2015), causing native plant and insect species loss, with stronger impacts for those that are not able to feed on the alien plants, due to temporal, nutritional or morphological limitations (Stout and Morales, 2009).

Nevertheless the effects of alien species on pollinator communities are not homogenous and vary with the traits of the invasive species themselves and on the composition of the native communities where they are introduced (Tiedeken & Stout, 2015). Moreover, alien and invasive species are often associated with the introduction of pests and disease (Ghazoul, 2005), such as, for example, the mite *Varroa destructor*, the Asian parasite originally affecting *Apis cerana* and now considered one of the most damaging enemies of honey bee colonies worldwide (Coffey, 2007), given its role as a vector for viruses between colonies.

Different groups of flower-visiting insect are associated with particular pests. Pests and diseases can damage flower-visiting insects, impacting their fitness in several ways, such as affecting the number of brood cells (Goodell, 2003), destroying their cells containing larvae (Felicioli, 2000), exploitation of their food resources (kleptoparasitism) or feeding on the hosts' larvae (Krunić et al., 2005). The load of infestation of population by parasitoids depends on many environmental variables, such as weather and habitat characteristics, as well as by the phenology and behaviour of the hosts and of its population dynamics (Jauker et al., 2012; Cohen et al., 2017; Ostap-Chec et al., 2021). In addition, the exposure to some chemicals was correlated to a change of the responses for the hosts, enhancing the risk of insects to pest and diseases infestation (Goulson et al., 2015).

1.2.4 Landscape degradation

One of the main drivers of flower-visiting insect decline is the degradation of habitat (Potts et al., 2010 a). Habitat loss and simplification, habitat isolation and fragmentation, conversion of semi-natural habitats into intensively managed habitats for agriculture and, in particular, monocultures, are all phenomena related with ecosystem degradation and with a consequent decline in biodiversity, including the richness, abundance and diversity of different groups of flower-visiting insects (Potts et al., 2010 a; Tscharntke et al., 2012; Goulson et al., 2015). In Ireland, for example, the major cause of the decline of bumble bee species was attributed to habitat loss and fragmentation and to a change of land use (from hay to silage production (Fitzpatrick et al., 2007).Where a strongly negative impact on the richness and abundance of wild bees was found with the increase in distance from semi-natural habitats (related to habitat loss and/or its conversion; Ricketts et al., 2008), evidence shows that different type of semi-natural, well connected and diverse habitats have positive effects on insects and pollinators in an agricultural context (Holzschuh et al., 2010; Klein et al., 2012; Griffin & Haddad, 2021; Maurer et al., 2022).

Changes in the landscape are often connected to anthropogenic activities, either occurring with the conversion of semi-natural habitats into monocultures or intensively managed fields, or following intensive urbanisation, or as a consequence of human-mediated climate change (Potts et al., 2010 a). The loss of habitat and its conversion can impact insects lives in different ways, for example limiting the habitats available for nesting, finding food, or mating (Potts et al., 2010 a; Goulson et al., 2015). A loss and homogenisation of habitats also affects the capacity of some species to complete their life cycles, because some insect groups, e.g. butterflies, need different types of habitats or plants during different moments of their development, and because different species of insects occupy different niches (Erhardt, 1985; Erhardt & Mevi-Schütz, 2009; Goulson et al., 2015). Moreover, habitats characterised by agriculture are often associated with intensive management techniques, with the use of pesticides, or with the fragmentation and homogenisation of the territory. Changes in habitats also impacts plant richness, abundance and distribution, with negative effects on insects and on plant-pollination networks (Potts et al., 2010 a).

However, despite general trends, the mechanisms regulating insect responses to habitat change are not homogenous and depend on the characteristics of the habitat itself, on the species considered, on the temporal and spatial scale studied. In addition, they might also change depending on the interaction with other drivers responsible for insects decline (Hadley &Betts, 2012; Kremen et al., 2012; Duuning et al., 2019; Potts et al., 2010 a; Goulson et al., 2015).

1.2.5 Interaction between the threats

Pesticides, pests and diseases, habitat loss and fragmentation, invasive species and climate change are the major threats that pollinators face. The risk that all these stressors pose for insects is enhanced by the fact that they are not independent. Their interaction can result in a more harmful effect on pollinator health compared to the impact of the single stressors. Moreover, the effect that a combination of stressors might have on insects is very difficult to predict and study (Becher et al., 2013; Goulson et al., 2015).

The first thing to consider about the interaction between stressors, is the parallel decline of pollinators and plant species. A decline in the number of pollinators, might negatively affect the abundance or richness of plant species (Biesmijer et al. 2006). The decrease in plant biodiversity enhances nutritional stress, associated with a further decrease in pollinators species. Climate change, invasive species and habitat loss and fragmentation are stressors that are connected to the loss of biodiversity of plants. For this reason, they are indirectly involved in the decreasing of pollinators' food resources, and thus they contribute to the ripple effect that is due to the combined stressors (Goulson et al., 2015).

In addition to the effect on diet caused by the lack of floral resources, a decline in plant biodiversity may also affect the susceptibility of bees to parasites and disease, and to the risk associated with pesticides (Potts et al., 2010 a; Goulson et al., 2015). The energy required by organisms to activate immune responses can be compromised by dietary stress, causing a reduction in the capacity to cope with toxins and pathogens. An example could be represented by *Crithidia bombi*, that causes little mortality in well-nourished bumble bees, but becomes virulent in those individuals that have a poor diet (Goulson et al., 2015). However, an increase in dietary intake may enhance the level of pesticides ingested in agricultural contexts where other food resources are lacking. Pesticides might interact with pathogens, ultimately impacting the immune systems. For example, bees exposed to neonicotinoid pesticides are more susceptible to *Nosema* spp. (Goulson et al., 2015). Moreover, the immunosuppression due to the exposure to the neonicotinoid can promote Deformed Wing Virus (DWV) replication in insects affected by this infection (Goulson et al., 2015). In some species, lack of food resources is also connected to higher energetic costs, consequent to longer foraging flights (Frey-Roos etal., 1995; Fryxell and Doucet, 1991; Orians and Pearson, 1979). A side consequence of longer foraging flight is a higher probability of brood cell attack by parasitoids depending on the time the cell is open and unguarded by the female bee (Ulbrich & Seidelmann, 2000; Bosch, 2008).

1.3 European land use

Between 50 and 75% of the land surface of the Earth is converted to human use (Winfree et al. 2009). The European landscape covers a large range of habitats and land uses and includes several biogeographic regions characterised by different environments, climate conditions and topography (Eurostat, 2018). A large proportion of the land is occupied by woodland (41.1%), with different characteristics – large and dense forests with low underground vegetation in the northern countries, and less dense forests characterised by shorter trees and dense understory vegetation in the southern regions (Eurostat, 2018). Over 47% (EEA Report No 10/2017) of land area is covered by farmland (24.4% cropland, 17.4% grassland and 5.7 shrubland; Eurostat, 2018). Of this, over 1/3 is constituted by grassland for livestock grazing or fodder (FAO, 2006), although the proportion of agricultural land devoted to grassland is different in the different regions (Lee, 1988), with Ireland being the only European country where more than half of its land use is devoted to such an habitat (Eurostat, 2018).

Livestock rearing requires green fodder from arable land (such as maize, beets, temporary grasses and grazing, clover and mixtures, lucerne and other types of legumes) and from permanent grassland (permanent meadows and permanent pastures, such as herbages or such as that used for rough grazing; Eurostat, 2001; Smit et al., 2008). Besides being associated with production, grassland areas also provide other ecosystem services like supporting the biodiversity and reducing erosion, buffering the effect of pesticides and fertilizer on water and regulating the regimes of the water areas, and contributing to cultural heritage (Hopkins and Holz, 2005; Reid et al., 2005; Smit et al., 2008).

Even though in the past, farmland used to support high biodiversity, from the second half of the 20th century, its intensification caused the decline of biodiversity, with a consequent impact on the delivery of several ecosystem services (Clavel et al. 2011; Scheper et al., 2013; Buhk et al., 2018; Senapathi et al., 2017). The intensification of farming has led to a more homogeneous environment, to an increase in the use of agrochemicals and to a decrease of the non-cultivated elements, such as hedgerows (Belfrage et al., 2005), and this could constitute a risk for biodiversity, including for flower-visiting insects.

1.3.1 A case study: Irish landscape and intensively-managed grassland

Habitats in Ireland are diverse and include arable fields, grasslands, hedgerows, streams, ditches, bogs, lakes, turloughs, rivers, native woodlands, forests and maritime areas (The Heritage Council and Teagasc; Sheridan et al. 2011). However, over 60% of Irish landscape, corresponding to 4.3 million hectares, is used for agriculture. While intensively managed crops are mainly located in the East of the country, the West is composed of small wet fields (Heritage Council and Teagasc; Hecq, 2016). About 10% of agricultural landscape is dedicated to arable crops (The Heritage Council, 2010; Hecq, 2016), and 14.3% to semi-natural habitats (Sheridan et al., 2011). The rest of the agricultural land is composed of grassland.

Most of the grassland is intensively managed (i.e. agriculturally “improved”), meaning it is highly modified, reseeded and fertilised for grazing and silage making (Fossitt, 2000; (Martin et al., 2007). According to Fossit, 2000 (Irish habitat classification) improved grassland is subdivided in two categories: improved agricultural grassland and amenity grassland. A small proportion of grassland is devoted to semi-natural areas and categorised by Fossitt, 2000, in four groups: Dry calcareous and neutral grasslands; Dry meadow and grassy verges; Dry humid acid grasslands; and Wet grasslands (Fossitt, 2000). The dry calcareous and neutral grasslands, typically grazed by livestock and developed over chalk and limestone, represents an important habitat for pollinators because of its flora diversity, occurring as a result of low intensity agriculture and on free draining mineral soils of various depths (Mullen, 2013; Falk, 2016). According to Sullivan et al. (2010) an intermediate category, semi-improved grassland, should be considered beside the intensive and semi-natural grassland. This type of land use is characterised by lower intensity of management (compared to intensively managed grassland) and by a medium level of species-richness.

Few crops in Ireland are entomophilous. Pollinator-dependent species are those present in orchards, such as apples, and some soft fruits, like strawberries, raspberries and blackcurrants. The main entomophilous field crop is *Brassica napus*, oilseed rape, an annual mass-blooming crop. There are two types of oilseed rape grown in Ireland (depending on their sowing time): spring oilseed rape (with an average yield of 2.2 tonnes per hectare) and winter oilseed rape (with an average yield of 4.2 tonnes per hectare). Oilseed rape crops are integrated in cereal rotation and are considered beneficial for improving the soil structure. Moreover, they are used for vegetable oil production and as fodder for livestock, while in the past they were used for bioethanol. Other bioenergy crops in Ireland are cereals, hemp (annual crop), willow, miscanthus, reed canary grass (perennial crops) (CSO, 2012; Department of Communications Marine and Natural Resources, 2007; Teagasc, 2009; Hecq, 2016).

Hedgerows are important semi-natural features in the managed landscape in Ireland. These are important for pollinators, because they are related to the provision of food, nest sites, shelter, corridors for movement and hibernation sites for fauna (Marshall & Moonen, 2002; Teagasc, 2004). Irish hedgerows provide habitat for 37 species of native and non-native shrubs and trees and for 105 species of wild herbaceous plants (Department of the Environment and Heritage and Local Government, 2007). However, Irish hedgerows are threatened. The main risks come from their clearance, promoted by agricultural intensification and an expansion of agricultural land (Curtis & McGough, 1988; Department of the Environment and Heritage and Local Government, 2007), or for urbanisation, and from their over-cutting to prevent their encroachment into the productive land in the field (Natural England, 2007). The loss of hedgerows affects the biodiversity of the environment and in particular damages the pollinators that feed on them (The National Trust for Ireland, 2011).

1.4 Landscape characteristics and flower-visiting insects responses

Landscape structure is defined by two aspects, compositional and configurational heterogeneity, both playing a key role in terms of impacting biodiversity (Fahrig et al. 2011; Hass et al. 2018;). The composition of the landscape describes the type of habitats and land uses of the different patches that constitute an area. The configuration of the landscape defines the spatial arrangements of those patches - their number, shape, connectivity, isolation, distance and boundaries; (Uuemaa et al. 2011; Flick et al. 2012; Hadley and Betts, 2012; Hass et al. 2018). Landscapes characterised by high compositional heterogeneity are highly diverse and offer more foraging and nesting resources, supporting a high number of species (Dunning et al. 1992; Fahrig et al., 2011; Flick et al. 2012). On the other hand, high configurational heterogeneity enhances landscape connectivity, offering important nesting sites and providing crucial elements for the movement of species and their orientation in the landscape, with consequences for population dynamics and on plant-pollinator interaction networks (Becher et al. 2016; Hass et al. 2018; Steffan-Dewenter and Tscharntke, 1999; Hass et al. 2018).

Hence, landscapes that are heterogeneous in both their composition and configuration seem to support biodiversity, including flower-visiting insect abundance, richness and diversity, influencing their movements, providing nesting sites and affecting temporal and spatial distribution of feeding resources, fundamental for supporting diverse stages of their life (Hristof 2002; Kremen et al. 2007; Fahrig et al. 2011; Cole et al. 2017; Senapathi et al. 2017; Hass et al. 2018). For example, hoverfly richness was found to be positively correlated with high compositional heterogeneous and well-connected landscape, and hoverfly richness was related to the abundance of local floral resources (Power et al., 2016). Similarly, Kennedy et al. (2013), found a higher wild bee species richness and abundance in high quality habitats (defined according to the models of Lonsdorf et al., 2009, as habitats characterised by a land cover that provides suitable land cover for bees).

On the other hand, habitats with low composition and configuration heterogeneity, are related to phenomena like fragmentation, habitat loss, and degradation of habitat quality, with consequent decrease of the number and quality of the resources (Fahrig et al. 1997; Uuemaa et al. 2011; Flick et al. 2012; Hadley and Betts, 2012; Marini et al. 2014; Senapathi et al. 2017; Hass et al. 2018). Structurally simple landscapes are associated with loss of pollinators, pollinator diversity and abundance (Senapathi et al. 2017), even though the responses of insects vary depending on their taxa.

The composition and configuration of the landscape are not separate entities and their interaction can impact biodiversity in different ways.

1.4.1 Habitat fragmentation, isolation and habitat loss

Studying fragmentation and its impacts on insect biodiversity is complex, mainly because there is a lack of precise definition of this phenomenon. Different authors define it and measure it in different ways, and at different scales. Generally speaking, fragmentation refers to the transformation of habitat into smaller patches that are isolated from each other. Nevertheless, fragmentation could involve isolation and habitat loss, or not. Habitat loss has a negative effect on biodiversity, adversely affecting species richness, population abundance and distribution, genetic diversity and the growth rate of populations (Fahrig, 2003). Similarly, isolation of habitat might negatively impact on biodiversity, constraining communities and preventing individuals from moving in the landscape, with consequences on the genetic pool and on potential access to food or nesting resources. The isolation and fragmentation of habitats were found to negatively impact on abundance of bee species, with a parallel decline in seed set (Hass et al., 2018). Conversely, a well-connected landscape (characterised by high coverage of hedgerows) was one of the characteristics positively impacting the hoverfly abundance in the study conducted by Power et al. (2016) in conventional and organic grasslands in Ireland. Similarly, habitat connectivity was found to be a necessary requirement to preserve bee communities and the insect-plant interaction in grassland patches located in intensively managed areas (Steffan-Dewenter and Tscharntke, 1999).

When fragmentation is associated with a reduction in the amount of habitat, it has negative impacts on species richness and their presence/absence. This is probably related to a decrease of habitat that can be used to forage or nest. Nagamitsu et al., (2018) for example, found a negative impact of the loss of natural broadleaved forests, caused by the conversion of these habitats to coniferous plantations, and on the foraging performances of a species of wild bee. Similarly, the sizes of patches following fragmentation might play a key role at sustaining or reducing species diversity. Thus, the combination of habitat loss and fragmentation creates areas too small to sustain populations and can prevent the movement of individuals between patches, with consequences for their mortality (Fahrig 2003). In fragmented landscapes, individuals are more likely to leave their habitat for the matrix, with negative consequences on mortality and reproductive rates. In addition, smaller patches can only contain a limited number of species (Fahrig 2003). Nevertheless, other evidence suggests that several small patches might better sustain populations compared with a single large patch, complicating the debate about the role of fragmentation in sustaining communities (Fahrig et al., 2021).

On the other hand, when the fragmentation phenomenon does not involve habitat loss, the creation of numerous patches might promote immigration and dispersal between different regions, resulting in the increase of the habitat diversity. This is also related to an increase in the number of edges, features related to high heterogeneity (Fahrig, 2003). In the agricultural context, the edges of fields might be important for biodiversity because they can be composed of floral species that constitute a semi-natural element that might provide food or nesting resources, promote the movement of individuals and their migration (in the case of hedgerows). Moreover, if the habitat area is constant (no habitat loss), an increase in fragmentation can result in shorter distances between patches with a reduction of the isolation (Fahrig, 2003). Nevertheless, the characteristics of the patches themselves, such as their areas or their density, can impact on biodiversity, when they interact with the characteristics of the population (Dauber et al., 2009).

Hence, the effects of fragmentation vary depending on how it transforms the landscape and if it involves isolation and habitat loss. However, it can be difficult to investigate the impact of fragmentation *per se*, separating this phenomenon from habitat loss. In a review, it emerged that the effects of habitat loss and fragmentation on pollination were separated only in six studies out of the 303 considered (Hadley & Betts, 2011).

In addition, different groups of insects might respond in a different way to these phenomena. Species that locate their nest below ground, species with a large flight distance and species with a broad diet seem to be less affected by the phenomenon of isolation. Smaller niche breadth species are more affected by fragmentation (Gathmann & Tscharntke, 2002; Williams et al., 2010).

1.4.2 Semi-natural areas and habitat diversity

Benefits provided by semi-natural habitats for supporting insects are well documented. At a landscape scale, woodlands and meadows have been associated with higher biodiversity. This also impacts on insect communities, positively correlating with both their richness and abundance. (Steffan-Dewenter and Tscharntke, 1999; Weibull et al. 2000; Rundlöf et al. 2008; Marini et al. 2012; Ghazoul, 2005). This is because semi-natural landscapes can provide more resources in terms of both nests and food (Goulson et al., 2015). In relation to this, some groups of insects are central-place foragers and they need to go back to their nests after collecting the food. The co-occurrence of good nest locations with food resources in semi-natural and diverse habitats might benefit these insects (Seeley, 1995; Dyer, 2002; Roulston & Goodell, 2011). Similarly, the presence of flowers in the vicinity of the nests can reduce foraging flight distances. Shorter foraging flights are correlated with lower energy costs, lower parasitoid load in some groups of wild bees, where the rate of infestation of the cells is positively correlated with the length of time females spend away from nests foraging, to provide food for the cells, with repercussions on the fitness of the population (Müller et al., 2006; Seidelmann, 2006; Zurbuchen et al., 2010; Roulston and Goodell, 2011). In addition, higher food availability given by the succession of different species' blooming periods through the year, can help to fill nutritional gaps, or to support species with different phenological requirements (Danner et al. 2016; Buhk et al. 2018: Timberlake et al., 2019). Different species might occupy different temporal niches, thus both the abundance and the diversity of the floral species may be necessary requirements to support insect biodiversity (Scheper et al., 2015; Timberlake et al., 2019; Russo et al., 2022). Moreover, even within the same species several habitats might be necessary to complete the life cycle of the individuals, given the needs for the species of different nieces for different moments of their lives (Erhardt, 1985; Erhardt & Mevi-Schütz, 2009). In addition, an increase in the proportion of natural habitats in the landscape surrounding cultivation, was found to buffer the negative impact of pesticides on bee abundance and richness in orchards (Park et al., 2015) and mitigate the negative effects of parasitism (Jauker et al., 2012). Thus, in the farmland context, the presence of semi-natural habitats in surrounding areas was positively correlated with the presence and richness of some pollinators (Kremen et al. 2002; Klein et al. 2012).

Besides being important at a landscape level, semi-natural habitats and habitat diversity play an important role at a local scale, where the presence of hedgerows, floral strips and shrubs, can positively impact communities of insects living in agricultural ecosystems. In European agricultural contexts, these field boundaries are usually formed by strips of different sizes, composed of semi-natural vegetation (Marshall and Moonen, 2002; Hass et al., 2018). These components of the landscape have a crucial role in terms of their agronomic and environmental functions, and their specific composition might be important both in terms of the local pollinator population size and in their occurrence (Marshall and Moonen, 2002; Kremen et al., 2007). In fact, these linear features contain the greatest botanical diversity within the agricultural context, but also a high diversity of mammals and invertebrates (Marshall and Moonen, 2002). Thanks to high plant diversity, these features provide floral resources that pollinators can use to feed, breed and nest (Marshall and Moonen, 2002; Hass et al., 2018). Indeed, even though permanent pasture and woodland produce the greatest amount of nectar in a farming landscape, because of large areas they occupy, hedgerows and field margins are the elements that provide the greatest amount of nectar per unit area (Baude et al. 2016; Timberlake & Vaughan, 2019)

Moreover, semi-natural margins provide a useful corridor that allows movement of individuals through the landscape, affecting their genetics and their behaviour (Marshall and Moonen, 2002; Hass et al., 2018). Another important role of the margins, that might have consequences on pollinators, is their buffer effect on the movement of pollutants between adjacent habitats (Marshall and Moonen, 2002). They are also responsible of influencing the flow of nutrients and water within the agricultural landscape (Marshall and Moonen, 2002).

In the agricultural context, the floral resources on the margins and in the surrounding landscape have an important role in sustaining pollinators after the flowering periods of entomophilous monoculture crops. Furthermore, their importance during the crop flowering period, as alternative source of floral resources, was proved (Hanley et al. 2011; Stanley & Stout, 2014). Specifically, wild flower strips appear to enhance species richness and abundance of wild bees (including Red List species) and to increase the number of species of butterflies (Buhk et al., 2018; (Scheper et al., 2015). The magnitude of this effect, though, seems to depend on the interplay between the enhancement of floral resources within the strips and their abundance in the landscape surrounding the crops, at different times of the year (Scheper et al., 2015). For example, positive effects of floral strips on bumble bees may be because they enhance landscape-wide floral resource availability early in the season. On the other hand, solitary bees decrease with an increase of floral resources availability in the landscape during the late season (Scheper et al., 2015). These different responses to the flower strips could be explained by a possible decreased attractiveness of the floral strips in the surrounding context characterised by high resource availability, where the foraging bees are more distributed over the landscape, showing a diluted pattern. Instead, in landscapes with low availability of alternative floral resources, there may be a higher concentration of pollinators on the flower strips. The study of Scheper et al. (2015), shows how the effect of the floral resources does not depend only on the spatial-temporal scale, but also on the taxon of the insects. Further evidence of this taxon-dependency effect, shows that the increase of the border density has a strong positive effect on wild bee abundance and seed set, even if it does not seem to affect other species such as hoverflies (Veddeler et al. 2006; Carvell et al. 2011; Holzschuh et al. 2011; Hass et al., 2018; Scheper et al., 2015).

These elements can, on the one hand, provide shelter and nest sites for insects, as well as food resources that might be otherwise be scarce in anthropogenic environments. On the other hand, these natural features can support insect migration and movement between patches, enhancing habitat connectivity of fragmented areas, with positive repercussion for the genetic pool of the species.

1.4.3 Agricultural crops and urban areas

Changing land use from semi-natural ecosystem to intensive agricultural ecosystem has greatly reduced the biodiversity of temperate and tropical regions, because of the loss and homogenisation of habitat, and the decline in floral abundance and diversity (Ghazoul, 2005). A conversion of semi-natural landscapes into intensive agricultural land use has been documented in Europe with a consequent loss and a homogenisation of the habitat (Ghazoul, 2005; Goulson et al. 2008). This conversion was associated with the occurrence of intensive management techniques, such as the use of chemicals, that have an elevated risk of toxicity for insects and with the occurrence of monocultures and mowing and silage techniques impacting on plants diversity (Potts et al., 2010 a; Goulson et al., 2015). In this sense, agricultural land use might constitute a threat for insect pollinator biodiversity, when it implies a reduction of the composition and the configuration heterogeneity of the habitat. Thus, agricultural landscapes have been associated with reduced biodiversity, including insects, and a decrease of semi-natural elements (Benton 2003; Ghazoul 2005; Goulson et al. 2008; Kennedy et al. 2013; Vanbergen et al. 2013; Bretagnolle et al. 2015; Senapathi et al. 2017), with consequences on the ecosystem itself (Cardinale, 2012).

However, other studies report a positive interaction between cultivation and insects (Westphal et al., 2003; Carrè et al., 2009; Holzschuh et al., 2012; Stanley & Stout, 2013). The type of crop and its management seem to modulate such a trend. Some mass flowering crops, for example oilseed rape crops, have been found to have positive impact on some groups of insects, like bumble bees and solitary bees, at some stages of the year, compared to other types of crops (Stanley and Stout, 2013; Holzschuh et al., 2013). This is probably related to the highly rewarding flowering resources that such crops provide to those insects active at the time of the blossoming (Suzuki et al. 2009; Scheper et al., 2015). However, despite being abundant, this blossoming is time-limited, thus the presence of monocultures can create eventual nutritional gaps later on in the season (Timberlake et al., 2019).

Besides crop type, another characteristic influencing the effects of agriculture on insects is associated with the type of management. Crops with long rotation period and low input have higher biodiversity of insects compared with high intensity annual crops (Stanley and Stout, 2013). At a local level, organic crops are related to higher biodiversity and higher richness and abundance of pollinators compared to conventional crops (Kennedy et al., 2013) Similar trends have been recorded across Europe and in several groups of insects. In Germany, pollinator species richness in organic fields was twenty times higher than in conventional crops, while their abundance was even more than one-hundred times higher (Krauss et al., 2011). In Ireland, diversity in hoverflies was correlated with farm management intensity, with organic farms having a higher level of richness and abundance of this taxon (Power et al., 2016). While in Sweden, the abundance and richness of butterflies present in organic farms appear to be respectively 60% and 20% higher than in the conventional ones (Jonason et al., 2011).

Overall, in their meta-analyses, Bengstsson et al., (2005) showed a general positive impact of organic management on insect richness of the farming areas, with increases of around 30% compared to conventional management. Similarly, out of the 117 studies analysed, 96 showed a positive effect of organic farming on abundance – insects were 50% more abundant than in conventional farming (Bengtsson et al., 2005; Belfrage et al., 2005). However, both the abundance and richness of insects due to organic management was taxon-dependent. Other characteristics of the crops might also interact with the type of management to shape insect communities. Kennedy et al. (2013) showed that, at the local scale, the abundance of pollinator communities seems to be positively influenced by both organic management and field diversity, with conventionally managed crops reported to have a similar abundance of pollinators compared with organic crops, when plant diversity in fields was high (Kennedy et al., 2013). In that study, diverse fields were those "< 4 ha, with mixed crop types within or across fields and/or presence of non-crop vegetation, such as hedgerows, flower strips, and/or weedy margins or agroforestry" (Kennedy et al. 2013). The same study also showed that high vegetation diversity in conventional crops had the same positive effect on the abundance of pollinators as organic fields that had low vegetation diversity (Kennedy et al., 2013).

Another aspect that influences biodiversity of pollinators is the size of crop fields. Belfrage et al. (2005) showed a higher abundance of butterflies and bumble bees with a decrease in field size, and with an increase in crop species diversity. This result might be the consequence of the higher heterogeneity of the landscape, correlated with small farms. At a crop level, the richness and abundance of insects also depend on the habitat surrounding the fields at a landscape level (Ricketts et al., 2008; Marini et al., 2012).

Moreover, the positive effect of organic farming on species richness and abundance is related to the scale at which impacts are measured. Thus, a positive effect is likely in intensively managed agricultural landscapes, but it is not necessarily expected in those small scale landscapes, characterised by diverse habitats (non-crops habitats and mixed cropped fields; (Bengtsson et al., 2005).

Hence, even though the management of the crops is very important in order to maintain biodiversity, animal communities are affected by scale, and their responses vary among taxa. For this reason, the organic farming system *per se* should not be considered the major driver of species responses. Many other aspects present in the agricultural landscape have to be considered in order to analyse the impact of the landscape on pollinator communities. These elements, for example, hedgerows and field margins, are fundamental in the maintenance of biodiversity (Bengtsson et al., 2005; Jonason et al., 2011). Moreover, responses of insects communities to agricultural intensification varies across regions, with impact of agricultural land-use intensity greater in temperate than in tropical or subtropical systems (Palma et al., 2016).

Similarly, anthropological habitats such as urban settlements have been associated with insect abundance and richness. Urban areas might be responsible for homogenisation of habitat and can drive habitat loss. On the other hand, some moderate degree of urbanisation (or agricultural land use) might have a neutral or a positive effect for pollinators (Theodorou et al. 2017). Urban areas can offer habitat heterogeneity with positive consequences for the foraging and nesting resources for insects. Similarly, gardens not subjected to mowing and planted with diverse floral species might support pollinators across time and offer them diverse food resources, when semi-natural habitats are limited (Leong et al. 2016). Nevertheless, native floral species and species of flowers, blooming for the entire activity periods of insects are preferred, to avoid the spread of non-native species and phenomena such as inbreeding, and to support insects to prevent nutritional gaps. Moreover, in urban areas where herbaceous species are less common, the presence of trees may complement the lack of food resources for polylectic species. An example is represented by the red mason bees (*Osmia bicornis*), who are shown to prefer specific pollen types belonging to species such for example oaks, willows, maples, and thus the presence of even singular tree belonging to these taxa might support population of red mason bees across the urban gradient (Splitt et al., 2021). In addition, a recent study of Slachta et al., (2020) comparing gardens with orchards found the domestic garden being associated with lower contamination of pesticides and thus a lower risk for some insects groups (Slachta et al., 2020).

1.5 Impact of spatial and temporal scales

Despite the general trends, populations of insects are not static through time, due to phenological characteristics of the species or to the effect of environmental factors in different periods of the year. Moreover, evidence shows that when considering different spatial scales, insects responses to the environment might be different. For these reasons, it is important when considering threats affecting some insects groups, that these might be influenced by other temporal or spatial factors, including the landscape surrounding the sampled area.

1.5.1 Shift of pollinators on a temporal scale

The arrangement and density of insect populations in the landscape vary seasonally and through different years, even in geographically restricted regions. These variations depend on environmental characteristics and the phenology of species (Roubik, 2001; Williams et al. 2001; Kremen et al. 2002). The variation in the population of insects along time, are not only seasonal, but might change in different years. The sex ratio for example, i.e. the ratio of females and males in the population, has been found to change through time for some groups of insects (Tepedino & Torchio, 1982). Moreover, the impact of some environmental factors might affect the population with repercussion for their fitness, impacting several generations. This is, for example, the case of chemicals used in apple orchards, that were correlated with a decline in bee abundance, one year following the application (Park et al., 2015). Flower-visiting insects need both nectar and pollen for their sustainability. Whist nectar is usually associated with the energy necessary for the adults to perform their activities, pollen is also consumed by adults (especially reproductive females for ovary maturation) and to the development and growth of the larvae. Thus, one of the main factors shaping insects communities is the distribution and the availability of the floral resources in the landscape (Cane & Sipes, 2007). Both bumble bees and hoverflies have been noticed to vary in their use of habitat depending on the floral communities (Cole et al. 2017). However, plants phenology changes following seasonal trends. For this reason, insects not only vary their spatial movements and fluctuations depending on plant distributions, but they also follow plants temporal rhythms – seasonal trends, assemblages, peaks of blossoming…

In this context, the agricultural landscape might represent a temporal threat for flower-visiting insects, making it difficult for some groups of flower-visiting insect to access food resources in specific moment of their life stages. Some mass-flowering crops (for example oilseed rape crops) are considered good food resources for insects, providing highly rewarding flowering resources and being positively connected to pollinators density at a landscape scale (Westphal et al., 2003; Holzschuh et al., 2012). Moreover, some of these flowering crops may provide food early in the season, positively impacting those species that begin their activities early in the season. Bumble bees, for example, are likely to be attracted by agricultural landscapes with abundant blossoming early in the season when the queens look for nesting sites; such colonies are generally associated with high numbers of workers (Suzuki et al. 2009; Scheper et al., 2015). However, when this high rewarding provision of food is not balanced by other floral species blooming later in the season in the surrounding landscape (provided by semi-natural habitats or urban gardens or floral strips), pollinator communities might encounter nutritional gaps. In fact, crops provision of food is usually limited in time, and being characterised by short flowering periods. Thus, the influence of mass-flowering crops on pollen provision appears to be crop specific and seasonal and their impact on the flower-visiting insects also depends on the spatial scale. A general lack of floral resources availability in some moment of the year negatively may impact on insects (Timberlake et al., 2019). Studying the honey bee waggle dance, that indicate the location and the distance of flower resources available in the landscape, Couvillon et al. (2014) found a fluctuation in the amount of sugar concentration in nectar through the months. A lower content was found in June, July and August. March and April were also characterised by low concentration of sugar, but the wideness of the range suggests a better quality of the available resources. Surprisingly, the summer was more challenging even compared with autumn, because of the availability of ivy (*Hedera* spp.), abundant all along Europe during the autumn, in both urban and rural settings (Ratnieks et al., 2014). Similarly, previous studies (Couvillon, Schurch, & Ratnieks, 2014; Requier et al., 2015), identified in June and July nutritional gaps for honey bees. Similar nutritional gaps were found studying bumble bees, in relation to the nectar availability in farms (Timberlake et al., 2019), where a non-linear trend in sugar availability was recorded. Six different periods were identified depending on nectar variation and its availability, but such a trend was not synchronized with the nectar demand in bumble bees, creating two ‘hunger gaps’ – the first one was in early March, and the second extended from August to October. The gap in March was related to the sugar demand required by newly emerged bumble bee queens that was although limited by a low nectar production. At the other end of the season, between August and October the production of sugar was relatively high, but not sufficient to support the demand of bumble bee colonies of those species that reach their growth peak in this timeframe (Timberlake & Vaughan, 2019). Nutritional gaps might increase as a result of the shift in plant phenology and the related shift in plant-pollinator interactions, as consequence of climate change (Rafferty, and Ives, 2011).

Similar seasonal fluctuations, related to landscape context, were found in the study of Danner et al. (2016). They reported that if the spring bloom of mass flowering crops is not matched with mixed flower resources from semi natural habitats later in the season, the amount of pollen necessary for honey bee colony growth and development is insufficient.

The end of the flowering period of the mass-flowering crops thus can negatively affect some species, forcing them to extend their flight distances, in order to find food resources. The consequence of this behaviour is a higher level of energy consumption for the foraging individuals (Danner et al. 2016). Honey bees and bumble bees may cope with such energetic costs, being long distances foragers, but other species with shorter foraging ranges might be more adversely affected by the end of the mass-flowering season. For these species, as well as for butterflies, different longevities of wild and cultivated floral strips and different seeding times might contribute to their success of life stages**,** supporting their activities during different times of the year (Danner et al. 2016; Buhk et al., 2018).

Ultimately, physiological stresses affect plant phenology and changing temperatures might affect the timing of flowering periods . Such a climate-induced phenological mismatch between orchards and multiple groups of pollinators have consequences for the abundance, diversity and species composition of insects (Kőrösi et al., 2018). Such a shift in the floral community related to climate change was investigated (Aldridge et al., 2011), shows the possible implications of the shift in the spatial and temporal patterns of the floral resources, caused by changing climate, on pollinators. The disruption of plant pollinator networks and may initiate possible extinction cascade (Grünewald et al. 2010) and it might particularly affect those insects that are active along the season or those that are restricted to single habitats (Aldridge et al., 2011).

Another consequence of the low seasonal amount of flower resources, related to the lack of semi-natural habitat, is increasing species competition. Danner et al. (2016) analysed the foraging frequencies of different insects groups across the year, finding that for honey bees, foraging frequencies were higher in semi-natural habitats during springtime and summertime, when there was limited proportion of this type of habitat in the landscape. This may cause competition for pollen resources between insect species, caused by a limited availability of semi-natural resources and by the preference of honey bees to feed on semi-natural features habitats (Danner et al. 2016). Similarly, Scheper et al. (2015) showed an apparent negative effect of flowering strips during late summer in floral-rich landscapes, with alternative foraging opportunities for bees. The phenomenon might reflect a wider distribution of pollinators in the landscape, compared to a higher concentration of individuals in environments with low availability of food resources (Carvell et al. 2011; Veddeler et al. 2006; Holzschuh et al. 2011; Scheper et al., 2015).

Thus, even if some seasonal and yearly shifts in insect populations are normal and depend on the phenology of the species, some measures can be adopted to reduce the risk of environmental factors (such as pesticide exposure or flower availability) on insects. In particular, a lower pesticide exposure correlated to organic management and the preservation of diverse and abundant flower resources through the whole season can prevent a decline of the population insects in agricultural context. This could be achieved with diversified cultivation and a reduction in monoculture cropping, and/or introduction, restoration and maintenance of florally diverse hedgerows and floral strips.

1.5.2 Scale effect and landscape interaction

Evidence shows that many ecological patterns change depending on the spatial scale of observation, including species richness, species distribution or extinction risk. Scale-specific responses might be connected to environmental factors or biotic process (Shmida and Wilson 1985, Wiens 1989; Hadley and Betts, 2012; Tscharntke et al., 2012). For example, species richness on a regional level may change in relation to climate impact, but at a local level, changes in species richness can be attributed to habitat and biotic characteristics (Willis and Whittaker 2002). For example, in the study of Keil et al., (2010) a difference in species richness of hoverflies through time emerged, but varied according to the scale analysed. Although, data recorded in different countries (Netherlands and UK) showed different trends – the increase over time of hoverflies in Netherlands was only recorded at a fine scale, while in UK, species richness increased at a coarse scale, but species losses were recorded at a fine scale. Similarly, butterfly richness showed different trends depending on the scale of studies, with an increase of 7.62% at a 20 x 20 km scale in UK, but a decrease on a national scale of 5% (Menendez et al. 2006; Konvicka et al. 2006; Klein et al., 2010). Greater butterfly diversity was found in habitats with a higher heterogeneity of the agricultural landscape at a small-scale (Weibull et al., 2000).

This suggests the importance of analysing landscape context at different scales to better understand the trends in insects communities, because the response of insects (in terms of richness, abundance and diversity) might change. Besides the role of management of the crop on biodiversity (e.g. the bee richness and abundance was enhanced respectively by organic management, and organic management and field-level diversity (Kennedy et al., 2013), evidence shows that at local level (for example at a crop level), the richness and abundance of insects also depend on the habitat surrounding the area at a landscape level. In particular semi-natural and diverse habitat seems to better support insects population in crops, in comparison with arable land uses (Marini et al. 2012, Ricketts et al., 2008; Winfree et al., 2009). In this context, the role of natural areas is important because it supports crop pollinators, providing vital foraging and nesting resources for population establishment and growth that otherwise would not be available in agricultural fields (Park et al., 2015). In meta-analysis of local and landscape effects on wild bees in agroecosystems, bee abundance and richness were found to be higher at a landscape scale when more high-quality habitats (LLI score; Lonsdorf et al. 2009; Kennedy et al. 2013) were surrounding the field (3 km radius); this effect was most pronounced in Mediterranean and tropical systems. Furthermore, in landscapes dominated by cultivation, semi-natural habitats also have the role of buffering the negative effects that pesticides can have on pollinator populations. This is probably connected to the greater provision of resources (Park et al., 2015). Many studies investigated the role of habitats at a landscape scale at supporting insect communities in agricultural crops. For example, landscapes surrounding apple orchards in Trentino (Italy; Marini et al. 2012) at different spatial scales (250m, 500m, 1000m, 2000m) were found to have an important role at shaping the communities of bees in the target crops, where a landscape dominated by forests supported the highest number of wild bees species, followed by landscapes grassland-dominated. On the other hand, landscapes dominated by apple orchards drastically reduced wild pollinators richness and abundance. However, this trend was taxon-specific since the abundance of honey bees showed to increase in orchards-dominated habitats (Marini et al., 2012). In addition, higher bumble bee richness and abundance was recorded when there was wider proportion of grassland rather than arable crops at a 1 km radius (Rundlöf et al. 2008), while a negative correlation was found between some Irish bumble bee species (such as proportion of *B. cryptarum* and colony densities of *B. lucorum*) and the amount of arable land, in 700m radius (Stanley et al., 2013). Similarly, bumble bee abundance increased with wider semi-natural habitats in the landscape and local flower abundance at a 1000-2000 m scale, while at 1500-2000 m scale the positive effect was on the overall abundance of pollinators (Nayak et al., 2015). Nevertheless, Steffan-Dewenter et al., (2002) did not find positive responses of bumble bees or honey bees richness and abundance to the increasing proportion of semi-natural habitats at different small scales (250, 500 and 750 m), even though a positive relationship emerged for wild bees richness and abundance. In addition, the presence of semi-natural habitats surrounding cultivation (apple orchards) was shown to buffer the effect of pesticides exposure on wild bee with positive impact on wild bee abundance and richness in the orchards (Park et al., 2015).

Other studies, conducted in California, showed that the rate of visitation by native bee species to watermelon, and the species richness of bees, were positively correlated to the proportion of natural habitat surrounding the sites (at a 1 km of radius; Kremen et al. 2002); and that wild bee species visited almond flowers only in orchards surrounded by semi-natural habitats or vegetation strips (Klein et al., 2012). Landscape can also be associated with honey bees colony size: an example is the positive correlation between the amount of forest cover in intensively managed agricultural landscape and the colony size of honey bees (Odoux et al. 2014; Danner et al. 2016).

However, (Westphal et al., 2003) suggested that there is no correlation between the amount of semi-natural habitat (considered at 12 different scales within a range from 250 m to 3000 m radius) and the density of bumble bees (study conducted in Germany; Westphal et al. 2003). At the landscape scale in fact, their densities appear to be correlated with availability of nesting sites and with the availability of food resources provided by short-lived but highly rewarding mass flowering crops (such for example oilseed rape crops; (Westphal et al., 2003). Indeed, in the agricultural context, where the resources for pollinators become increasingly sparse, mass-flowering crops have positive impacts on bumble bee abundance and density, and on their colony growth (Westphal, et al. 2003; (Stanley et al., 2013; Westphal et al., 2003). Thus, sometimes, the effect of anthropogenic land use may be positively correlated with the richness and the abundance of insect populations. A moderate degree of urbanisation and agricultural land use might have a neutral or positive effect on pollinators. This might happen because such landscapes could potentially increase the landscape heterogeneity, providing pollinators with novel foraging and nesting resources, with the consequence of supporting pollinators biodiversity and pollination service (Theodorou et al., 2017). Leong et al. 2016 showed some beneficial effects of the urban areas adjacent to natural areas, in California. According to this study, an extended flowering season in urban areas might support bees when resources in natural habitat are limited, offering food supply at the earliest and latest portions of the season, maintaining a consistent richness of bee species through time (Leong et al., 2016). A study conducted in Arizona by Cane et al. (2006), on 62 different species of bees showed that some species of cavity-nesting bees were over-represented in the urban habitat fragments. This result could probably be attributed to the availability of enhanced nesting opportunities in the urban matrix (Cane et al., 2006). Another hypothesis suggests that the lack of a negative effect of the urbanisation on bee populations could be connected to the fact that a long history of human agriculture has already driven species sensitive to land use to extinction (Dormann et al., 2008).

In general, these studies show the complexity of the responses of pollinators to landscape heterogeneity. Differences in the responses of different insect taxa to landscape heterogeneity can depend on their ecological traits life history, body size, floral and nesting preferences, but also on the ecological traits of the plants they feed on, such as the length and timing of the flowering period, the flower abundance and the pollen and nectar quality. These studies also emphasise the benefit of adopting standard protocols when studying insects, given the impossibility of comparing results when the spatial or temporal scales are different.

1.6 Research questions

Despite general trends, pollinator communities respond to landscape characteristics in different ways. The same habitat or feature can have a different impact on insect pollinator communities, depending on the taxa, on the scale of area analysed, and on the managements techniques adopted for specific land uses (Senapathi et al., 2017; Theodorou et al., 2017). The different responses of pollinator groups to the landscape might be due to differences in their diet, behaviour, or preferences for floral resources, nesting, mating and overwintering sites (Gathmann and Tscharntke, 2002; Fenster et al., 2004; Klein et al., 2006; Cane et al., 2006). On the other hand, a landscape feature may not affect populations of all species in the same way, thus having potential impacts on abundance, richness and community composition/structure.

The interaction of different environmental and climatic factors, and the proportion of other habitats surrounding the area as well as its connectivity, might impact on insect communities, shaping their responses to specific land use types. A recent review analysing the combined effect of edge density and semi-natural habitat (configuration and composition features) on the abundance of different taxa around Europe, showed that their responses vary depending on the interactions of the composition and the configuration of the landscape and on taxon-specific response traits (Martin et al.2019).

Hence, studying the insect decline and status across Europe is complex. Studies are often limited to specific regions or insects groups. Moreover, studies might differ relatively to the temporal and/or spatial scales at which the experiments are set, preventing the comparison of the data to draw strong conclusion. Moreover, in landscape-scale studies several environmental variables should be considered, given the fact that their interaction can impact on the insects responses. Here the need of adopt a standardise method to investigate landscape impact on flower-visiting insect groups across Europe.

One of the biggest limits to studying the impact of the environment on insects is the difficulty in extending studies across a broad geographic and taxonomic scale. Studies comparing the responses of different insects groups, on big geographic regions are still rare. On the other hand, studies considering more countries are often based on meta-analyses that include studies that adopted different protocols for collecting the data (e.g. monitoring the insects through transects, pan-traps, observational quadrats; using different target crops or insects groups, including crops with different managements techniques). Adoption of unique protocols on European scale would help to fill some of the gaps in the literature, making it easy to compare data on a continental level. Moreover, in agricultural landscape the change of the mass-flowering crops through the season, as well as the phenological changes happening in the floral communities at a crop level, might interact with the phenology of insect populations. Moreover, insects have different life stages and the impact of the environment on these stages might imply changes in fitness.

My research was conducted as part of the PoshBee project (Brown et al., 2021; www.poshbee.eu), a study investigating the role of the multiple stressors on different groups of insects, at different times of the year, and of the development stages of the insects, at different scales. In addition, thanks to the adoption of unique protocols extended to several countries across Europe, PoshBee enabled a common approach to data collection. Specifically, in one of our studies, the landscape was analysed at different temporal scales (3 seasonal periods) and in different local context (crop margins vs centre of the cultivated crops). Moreover, in our study, the temporal context was addressed through the study of different life stages of one species of bee. In addition, two of our studies analysed analogue insect communities in cultivated crops, but at different geographic scales (at crop/field level and at a 1 km radius surrounding crop fields). The participation of 14 European countries, either for the data collection or for the analysis of the data, provided us with a wide dataset of variables at different scales, making it possible to investigate the impact of landscape on 5 different insects groups on a continental level.

My thesis addresses three main questions:

1. **What is the impact of crop type, surrounding landscape structure, and climatic variables on five groups of pollinating insects across Europe?** The role of the landscape surrounding agricultural crops in shaping five groups of insect communities, was investigated in two target crops, in eight countries, encompassing 4 biogeographic regions of Europe. Data were collected from 128 sites, and the impact of 18 environmental variables was analysed, including both composition and configuration landscape features (at 1 km radius) and weather and climate data. The adoption of the same sampling method (transects), both on the margins of the crops and in their centres, along with the decision to focus on five groups of insects (honey bees, bumble bees, solitary bees, hover flies, and butterflies) and on two common crop types (oilseed rape and orchards), gave us the opportunity to compare the dataset on a continental scale. In addition, the decision to use both compositional and configurational features of the landscape (such as percentage of less-intensively and semi-natural areas, urban areas, orchards area, isolation, habitat diversity…), in combination with climate and weather data, gave us the opportunity to analyse the difficult mechanisms regulating the communities of insects in agricultural context. Our hypothesis stated that less-intensively manged habitats, along with diverse and well-connected habitats, at a 1 km radius around the crops, could support the communities of insect in the target crops, positively impacting on their abundance. Conversely, we thought that agricultural and orchards crops, and urban habitats, and isolated patches of different land-uses would have been negatively correlated with the abundance of the target studied species in the crops. Our results showed that insects were responding to landscape and climate parameters in taxon- and crop-specific ways. However, less-intensively managed habitats (i.e. woodland, grassland, meadows, and hedgerows) and habitat diversity, positively impacted the insect groups with the total abundance of the five groups of insects, and the abundance of bumble bees and butterflies positively responding to the presence of less-intensively manged habitats surrounding the oilseed rape crops, and the abundance of solitary bee in oilseed rape fields, and of syrphid in apple orchards positively responding to habitat diversity.
2. **How do floral resources in two entomophilous crops affect five groups of flower-visiting insects in Ireland?** In our second study we decided to move the focus from a 1 km radius scale to a crop scale, studying the impact of the landscape on the communities of insects at a crop level. This time the location of the crops (oilseed rape and apple) was in Ireland, where 80% of the agricultural landscape is characterised by intensively managed grassland, representing a unique case study in Europe. In this context, we decided to investigate the role of the floral communities along the margins of the crops on the five target groups of insects in the crops, investigating differences between the margins of the fields and their centres in 11 oilseed rape and apple crops. In this context, we decided to consider the temporal scale too, investigating an eventual parallel change between the floral and insects communities

across three different periods (during the crop flowering period, approximately one to two months after the crop flowering period, approximately three months after the crop flowering period). In our study, the presence of flowered margins along the crops emerged as a semi-natural feature important for the insects communities in the crops. In fact, despite no temporal parallel shift between the plants and insects communities, both hoverflies and butterflies were found to be more abundant along the crops margins rather than in their centre, even during the bloom peak of the mass-flowering crops, that constitute abundant food resource.

3. **How do surrounding habitat and floral resources affect pollen collection and fitness in a solitary bee species across Europe?** In the third study we decided to focus on one species of flower-visiting insect common in Europe (*Osmia bicornis*). The adoption of a common protocols in six European countries, and the collection of the data across ninety-six sites, gave us the opportunity to analyse how the habitat surrounding the nests of *O. bicornis* impacted on the pollen stock in the nests, in terms of pollen diversity and botanical origin (pollen from crop species or not-crop species of plants). In addition, we analysed the relationship between the percentage of pollen of non-crop origin and the developmental stages of the bees, to evaluate the indirect role of the landscape on the fitness of this species. From this study, a positive impact of the non-cultivated habitats on the percentage of non-crop pollen in the nest was found. Our results also showed that more adults of *O. bicornis* hatched in those sites where the percentage of pollen of non-crop origin was higher. If from one side these results show the importance of non-crop pollen on the fitness of wild bees, on the other hand they suggest an indirect role of non-cultivated landscape on the bee fitness.

Overall the three studies, the positive impact of semi-natural and less intensively managed habitats, as well as habitat diversity, on insects in agricultural context was revealed, both at a 1 km radius (where such a landscape was represented by the percentage of less-intensively manged and diverse habitats) and at a crop level (where it was represented by the floral communities along the field margins). Similarly, the studies show the indirect impact of semi-natural habitats (represented by percentage of non-cultivated habitats at a 1 km radius) on *O. bicornis* communities, thanks to the provision of pollen from wild species of plants. Our study also shows differences between the two types of crops, with oilseed rape crops having a more positive effect on the fitness of different groups of insects, compared with apple orchards. In addition, our studies confirms that insects' responses to the habitat are strongly related to their taxa.

CHAPTER 2

Impact of landscape configuration and composition on pollinator communities across different European biogeographic regions

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2.1 Abstract

Heterogeneity in composition and spatial configuration of landscape elements support diversity and abundance of flower-visiting insects, but this is likely dependent on taxonomic group, spatial scale, weather and climatic conditions, and is particularly impacted by agricultural intensification. Here, we analysed the impacts of both aspects of landscape heterogeneity and the role of climatic and weather conditions on pollinating insect communities in two economically important mass-flowering crops across Europe. Using a standardized approach, we collected data on the abundance of five insect groups (honey bees, bumble bees, other bees, hover flies and butterflies) in eight oilseed rape and eight apple orchard sites (in crops and adjacent crop margins), across eight European countries (128 sites in total) encompassing four biogeographic regions and quantified habitat heterogeneity by calculating relevant landscape metrics for composition (proportion and diversity of land-use types) and configuration (the aggregation and isolation of land-use patches). We found that flower-visiting insects responded to landscape and climate parameters in taxon- and crop-specific ways. For example, landscape diversity was positively correlated with honey bee and solitary bee abundance in oilseed rape fields, and syrphid abundance in apple orchards. In apple sites, the total abundance of all pollinators, and particularly bumble bees and solitary bees, decreased with an increasing proportion of orchards in the surrounding landscape. In oilseed rape sites, less-intensively managed habitats (i.e. woodland, grassland, meadows, and hedgerows) positively influenced all pollinators and bumble bees and butterflies in particular. Additionally, our data showed that daily and annual temperature, as well as annual precipitation and precipitation seasonality affects the abundance of flower-visiting insects, although, again, these impacts appeared to be taxon- or crop-specific. Thus, in the context of global change, our findings emphasise the importance of understanding the role of taxon-specific responses to both changes in land use and climate, to ensure continued delivery of pollination services to pollinator-dependent crops.

Key words: Habitat heterogeneity, intensity gradient of land-use, pollinators, standardized approach, European biogeographic regions

2.2 Introduction

Flower-visiting pollinating insects provide a vital ecological service, contributing to the pollination of both wild and cultivated plants (Ollerton et al., 2011). However, in recent decades, a decrease in the abundance and diversity of insect pollinator taxa has been recorded across different regions of the world (IPBES 2016). Across Europe, between 37 and 65% of wild bee species are considered of conservation concern (Patiny et al., 2009; Nieto et al., 2014; Bretagnolle & Gaba, 2015), and a decline in bumble bee species richness has been documented for the last 60 years (Goulson et al., 2008). According to the European Red List of Butterflies, up to 10% of the butterfly species are considered threatened or nearly threatened (van Swaay et al. 2010, van Swaay et al., 2011; Warren et al., 2021), and over one-third of the European hover fly species are threatened as well (IUCN Red List, 2022). Scenarios of global change project further loss of butterflies (Settele et al., 2008), hover flies (Miličić et al. 2018), and bumble bees (Rasmont et al. 2015), supported by observed responses to historic climate change (Kerr et al., 2015).

These declines of pollinators are caused by multiple stressors (e.g. pesticides, climate change related factors, pathogens, invasive and alien species), with anthropogenic land use often considered as the main threat to flower-visiting insects (Goulson et al., 2008; Potts et al., 2010 a; Scheper et al., 2013; Winfree et al., 2009, Proesmans et al., 2021). Two main aspects of land use have been shown to affect biodiversity: compositional and configurational heterogeneity (Fahrig et al., 2011). The composition of the landscape describes the amount and the diversity of habitats or land use types that constitute the landscape; whereas the configuration of the landscape defines its spatial arrangement, e.g. the number and distribution of patches and their shapes, or their connectivity (Seppelt et al., 2016).

Landscapes characterised by high compositional heterogeneity are more diverse, and might offer additional foraging and breeding resources, and thus may support higher numbers of species (Dunning et al., 1992; Flick et al., 2012). In addition, high configurational heterogeneity enhances landscape connectivity, providing crucial structural elements for the movement of species and their orientation within the landscape, with positive consequences for population dynamics (population genetic structure and demography) and community interactions (Steffan-Dewenter & Tscharntke, 1999; Becher et al., 2016; Dominik et al., 2018; Hass et al., 2018). Thus, landscapes that are heterogeneous in both their composition and configuration are expected to support higher biodiversity, e.g. flower-visiting insects communities, by facilitating their dispersal providing extra nesting sites, and positively affecting the temporal and spatial distribution of floral resources (Steffan-Dewenter et al., 2002; Kremen et al., 2007; Fahrig et al., 2011; Cole et al., 2017; Senapathi et al., 2017; Hass et al., 2018). Conversely, habitats with low composition and configuration heterogeneity are usually associated with phenomena like fragmentation, habitat loss and degradation, which can result in the decrease of resource availability (Senapathi et al., 2017) and have negative impacts on flower-visiting insect movement, diet, reproduction, survival, and interaction with plants (Day 1991; O' Toole 1994; Hadley & Betts, 2012; Steffan-Dewenter & Tscharntke, 1999; Gathmann & Tscharntke, 2002).

Although the conversion of semi-natural land to intensive agriculture leads to habitat loss with adverse consequences for flower-visiting insects (Senapathi et al., 2017), the landscape surrounding cultivated crops may still support insect communities, depending on its composition and configuration (Bourke et al., 2014; Cranmer et al., 2012; Kennedy et al., 2013; Rundlöf et al., 2008; Steffan-Dewenter et al., 2002). Semi-natural landscape features, hedgerows and field margins in particular, can promote insect diversity by providing additional food or nesting resources, and facilitating the movement of individuals between patches (Bengtsson et al., 2005; Fahrig, 2003; Hole et al., 2005; Jonason et al., 2011; Marshall & Moonen, 2002). Mass-flowering crops can also be attractive to flower-visiting insects, by offering food resources with short-term beneficial effects for pollinators (Holzschuh et al., 2016; Jauker et al., 2012; Westphal et al., 2003), while floral strips, hedges, bushes and field margins can fill nutritional gaps outside the blooming periods of these crops (Bottero et al., 2021; Timberlake et al., 2019).

Despite overall negative impacts of agricultural intensification on insect communities, different taxa may respond differently to landscape heterogeneity and land-use intensity due to the disparities in their diet, behaviour, floral resource preferences and, nesting, and overwintering sites (Gathmann & Tscharntke, 2002; Fenster et al., 2004; Cane et al., 2006; Klein et al., 2007). A recent meta-analysis analysing the combined effects of edge density length and percentage of semi-natural habitat on the abundance of different arthropod taxa across Europe, showed that the responses were highly context dependent (Martin et al., 2019). In large-scale studies covering multiple biogeographic regions, contrasting responses of landscape heterogeneity on insect communities may also be a result of varying weather conditions (daily temperature, wind, rain) and climate (annual temperature and precipitation, precipitation seasonality). Weather and climatic conditions can either have direct effects, by affecting the survival and fitness of individuals, or indirect effects, by impacting the availability of foraging resources and the phenology of both insects and plants (Brittain et al., 2013; Lawson & Rands, 2019; Martinet et al., 2021; Vicens & Bosch, 2000), with consequent cascading impacts on plant-pollinator interactions (Hegland et al., 2009; Vasiliev & Greenwood, 2021). While the responses of insects to these effects are mostly taxon-specific, they also differ according to the temporal (daily, seasonal, between years) and spatial scale, as landscape structure can buffer climate impacts (Papanikolaou et al., 2017; Herrera, 2019; Zoller et al., 2020; Ganuza et al., 2022). However, studies investigating the complex suite of landscape and environmental factors that influence flower-visiting insect communities over a larger (e.g. European) biogeographic scale are still scarce.

In this study, we investigated the impact of both the composition and configuration of the landscape on the abundance of several broad taxonomic groups of flower-visiting insects, in 128 crop dominated sites across Europe. At the landscape scale, we hypothesised that more heterogeneous landscapes, with a larger proportion of less-intensively managed habitat (i.e., non-crop and non-urban), and less isolated habitats sustained a greater abundance of flower-visiting insects. At the field scale, we hypothesised that mass-flowering crops and orchards adjacent to the sites could supplement flower-visiting insect abundance, by providing them with additional resources at the beginning of the spring season. In the face of climate change, we also investigated the effects of weather and climate on the abundance of different pollinator insect groups, distributed across multiple biogeographic regions.

2.3 Methods

2.3.1 Experimental design

Eight countries were selected within the PoshBee site network (https://poshbee.eu/; Fig. 1), representing four of the main European biogeographic regions – Switzerland (CHE) and Germany (GER) for the Continental zone; Italy (ITA) and Spain (ESP) for the Mediterranean zone; Britain (GBR) and Ireland (IRE) for the Atlantic zone; and Estonia (EST) and Sweden (SWE) for the Boreal zone. In each country, we selected 16 sites according to a gradient of land use intensity: eight sites containing annual crops – winter-sown oilseed rape (OSR; *Brassica napus*) – and eight sites with perennial crops – apple orchards (APP), for a total of 128 sites (Fig. 1; Hodge et al., 2022). The land use intensity gradient was defined by the proportion of cropland and orchards within a 1 km radius of the centre of the sites (Hodge et al., 2022). We ensured a minimum distance of 3 km between the sites to avoid overlapping landscape buffers and violation of spatial independence for subsequent analyses (Hodge et al., 2022). Because of the large geographic range, and differences in cultivation patterns across this range, field sizes varied considerably: apple orchards varied between 0.32 and 45 hectares, while oilseed rape crops varied between 0.5 and 135 hectares (Hodge et al., 2022).

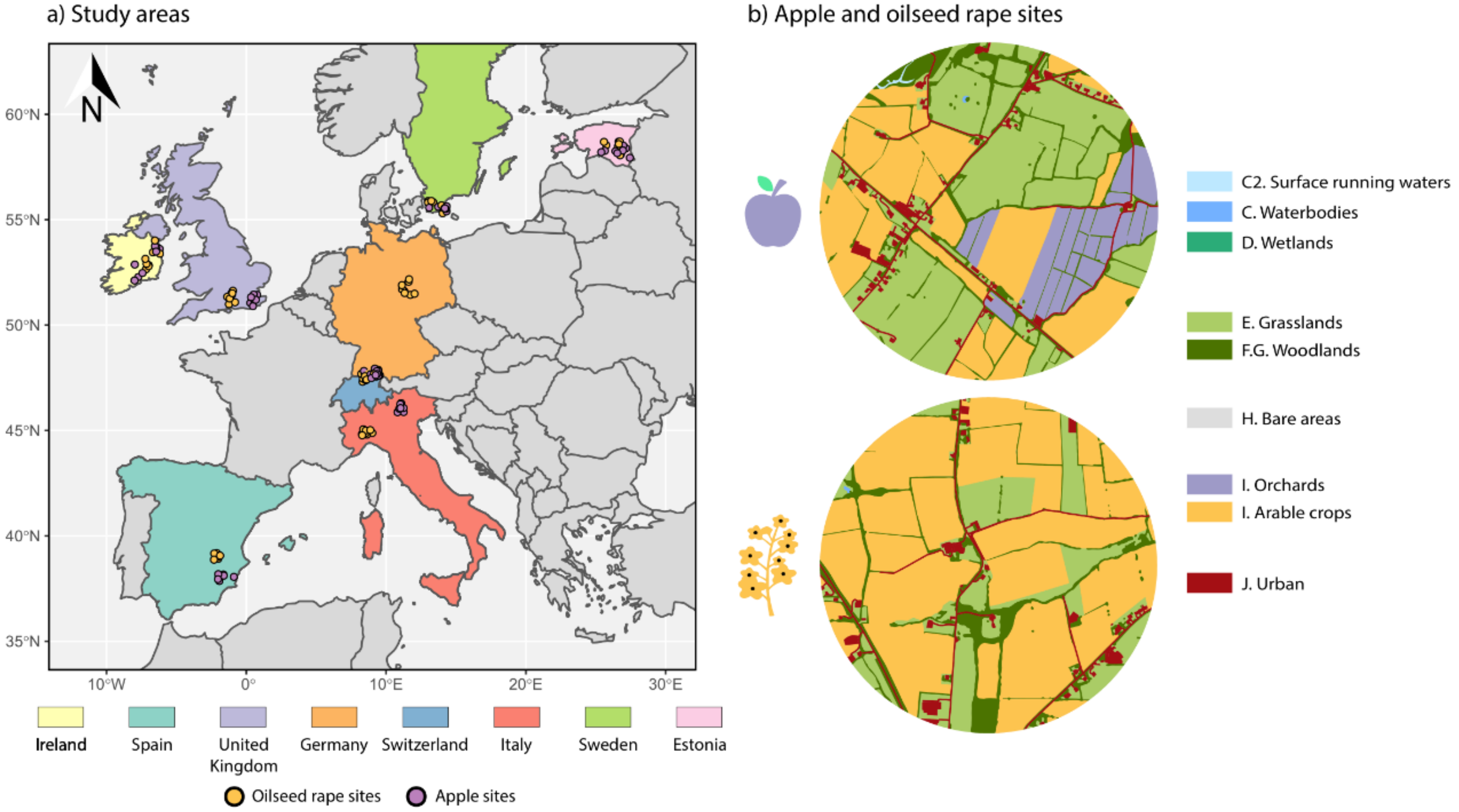

Figure 1. a) Location of the 128 sites – oilseed rape sites (orange dots) and apple sites (purple dots) across the eight countries. b) Examples of mapping land cover features within 1-km radius buffers around apple and oilseed rape sites.

2.3.2 Insect surveys

We selected five groups of obligate flower-visiting insects – honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), bees other than honey bees and bumble bees – here called solitary bees (despite the fact that some of them might be primitively eusocial, communal or kleptoparasitic species) (Hymenoptera, Apoidea, Anthophila), hover flies (Diptera, Syrphidae), and day-flying butterflies (Lepidoptera).

Insects belonging to the five groups were recorded along four transects per site. Two transect were placed in the centre of the focal crop field or orchard and two along the respective margins. The two transects in the centre of the crops were at least 30 m apart, as close as possible to the centre of the field. When this was not possible, they were at least 30 m from the edges of the field. The two transects on the margins were performed on the actual field borders (e.g. strips along the side of the crop, hedgerows, ditches, stonewalls, etc.). We surveyed the field borders rather than the edges of the crop itself, because our aim was to focus on landscape-level features, rather than to analyse variation within the crop field. Each transect was 50 m long and 2 m wide and walked for 5 minutes on three occasions during the main crop flowering period – at the beginning, peak and towards the end of flowering, resulting in a maximum of 12 transect walks per site. Transect walks were conducted from the 1st of April 2019 (oilseed rape in Ireland) to the 7th of June 2019 (oilseed rape in Germany; Appendix I). Insect surveys were only performed during suitable weather conditions, and between 10.00 am and 4.00 pm (see Mahon & Hodge, 2022). Due to unfavourable weather conditions or the difficulties accessing the centre of the crops at specific growing stages, 1,295 transect walks (84%) were completed (out of a possible total of 1,536). Transect walks were performed in a non-destructive manner (Hodge et al., 2022), which prevented a species-level identification, but allowed for the assessment of taxon-specific abundances.

2.3.3 Landscape heterogeneity

At the field scale, we identified the habitat type surrounding the focal sites, based on categories defined by the EUNIS habitat classification system (Davies et al., 2004), and recorded the number of the site borders with adjacent mass-flowering crops and orchards (such as apple orchards, oilseed rape crops, horticulture other than apples, and other types of crops e.g. peas) *in situ*.

At the landscape scale, we quantified different aspects of landscape heterogeneity by calculating multiple metrics that best describe habitat composition and configuration. First, all landscape features were manually digitalized at a 1:2500 scale within a 1 km radius around the sampling sites (Fig. 1), using a combination of head-up digitizing remote sensing data provided by World Imagery (ESRI) and GIS tools (ArcGIS Pro 2.4.1, ESRI). Following the EUNIS habitat classification reference, we classified all land cover categories into nine final categories: Surface Running Waters, Waterbodies, Wetlands, Grasslands (including both managed grassland for livestock, and semi-natural grassland), Woodlands (including also hedgerows, shrub plantations, lines of trees and gardens), Bare Areas, Orchards, Cropland, and Urban Areas (including different types of sealed areas such as roads and cities), see below and Fig. 1. Although, the EUNIS reference offers a detailed classification of each land-cover that best defines ecological habitats, we harmonized and reclassified the land cover categories in accordance with the habitat requirements of flower-visiting insects. Therefore, woodlands and hedgerows were combined into the same land-use cover class, under the assumption that they both positively benefit flower-visiting insects, by providing potential additional nectar, pollen or nesting resources (Marshall & Moonen, 2002, Marini et al., 2012, Alison et al., 2021). In contrast, sealed areas (urban areas of different intensity gradient) were grouped within the same land use type, as they may be an impediment to the survival of flower-visiting insects.

As a measure of compositional landscape heterogeneity, we measured the proportion of cropland, orchards, urban areas and less-intensively managed habitats (aggregation of wetland, woodlands and grasslands habitat types; Appendix II). Given the resolution of the habitat classification in our study, it was not possible to distinguish between highly managed grasslands (including pastures and silage fields) and semi-natural meadows, and between commercial forestry and woodlands, thus these land-uses were aggregated into less-intensively managed habitats. In addition of the proportion of cropland, orchards, urban areas and less-intensively managed habitats, we calculated a measure of landscape diversity (Shannon diversity index, SHDI) using all nine final land-cover categories (Appendix II). Landscape diversity is generally perceived as a critical aspect of landscape heterogeneity, as many arthropods may be associated with a single land use category (e.g., pollinators respond positively to semi-natural habitats).

As a measure of configurational landscape heterogeneity, we used the number of patches (NP) for orchards and cropland, as a proxy for the fragmentation of those habitats (Appendix II). In addition, we calculated the Interspersion and Juxtaposition Index (IJI), which describes how the different land use types are mixed together in the landscape; and habitat isolation (using the coefficient of variation of Euclidean Nearest-Neighbour distance – ENN), which calculates the distance between near patches belonging to the same land use type – calculated separately for cropland, orchard and less-intensively managed patches. We did not include edge density in our analyses, despite the established use of this measure for the assessment of configuration heterogeneity of the landscape, as it was strongly correlated with the proportion of less-intensively managed habitat. Configurational and compositional landscape metrics were calculated with the R package “landscapemetrics” (Hesselbarth et al., 2019).

2.3.4 Weather and climate parameters

Temperature was measured in the field during each sampling, at 1 m above the ground level in the shade, using a thermometer (Appendix II). For each site, long-term climate parameters (30 years averages from 1970 to 2000; spatial resolution approximately 1 km^2), related to multi-annual temperature and precipitation variables (such as the annual mean temperature and precipitation, or the precipitation seasonality which expresses the variation in monthly precipitation over the year), were extracted from the WorldClim database (v2.1; Fick & Hijmans, 2017; Appendix II).

2.3.5 Statistical analyses

The impacts of landscape structure, weather and climatic conditions on the abundance of the different insect groups were assessed using generalised linear mixed effects models (GLMM) with a Poisson distribution and a logit link, using country as a random factor (Appendix III). Because of the disparity in the insect surveys performed between countries (Appendix I), we pooled insect count data per site and used the number of visits to each site as an offset in the GLMMs. We calculated the models for the different pollinator groups separately and for all pollinators pooled. However, we removed the *A. mellifera* counts from the 'Total insects' group, due to possible bias related to the experimental placement of three honey bee colonies in each site (Hodge et al., 2022), and possibly elsewhere in the surrounding area (due to the pervasive presence of beekeeping in many of the landscapes), and because of their high abundance in the samples (70%; Fig. 2).

Due to the co-occurrence of other experiments at the moment of sampling, notably the presence in each site of three honey bee hives, three *Bombus terrestris* colonies and three *Osmia bicornis* trap nests, we did not directly compare the different groups of insects in an overall model (Hodge et al., 2022). Instead, we used separate models for each of our response variables: total number of insects (excluding *A. mellifera*), *A. mellifera, Bombus* spp., solitary bees, hover flies, butterflies, and for the two types of crops (oilseed rape and apple). We tested for multicollinearity between our initial set of explanatory variables, by using the variance inflation factor (VIF). A total of 18 variables were included as explanatory variables in the initial models (Appendix III). Because of the potentially strong impact of climate on the phenology of crop plants (Hegland et al., 2009), we considered potential interactions between annual temperature and the number of mass-flowering crops and orchards in the area adjacent to the sites, and landscape diversity, as well as an interaction between annual precipitation and mass-flowering crops and orchards (Appendix II).

In case of overdispersion, we added an observer term to the random structure (Harrison, 2014). To avoid overfitting, we limited the maximum number of terms to 6 (ca. 10% of data points). When the model failed to converge and the variance of "country" as random factor was negligible, we removed "country" as a random factor from the model. For each analysis, the final selection of the best model was conducted following a multimodel inference approach (Burnham & Anderson, 2002); dredge function of the MuMIn R package (Multimodel inference approach). Finally, we ran model diagnostics to test if all statistical requirements were met for each model and checked for spatial autocorrelation ("check_model" and "testSpatialAutocorrelation" functions in "performance" and "DHARMa" packages (Lüdecke et al., 2021).

To test for differences in total insect abundances between the two crop types (oilseed rape and apple), we used generalised linear mixed effects models (GLMM) with a Poisson distribution and a logit link, for each insect taxon, where crop was the independent variable and the country as a random intercept.

All analyses were performed using R software Version 1.3.1093 (R Core Team, 2020). We used the libraries “ggplot2” and “effects” for the construction of the graphs (Wickham, 2016; Fox, 2019), and the libraries “vegan” and “RcolorBrewer” for building the PCA plot (Oksanen et al, 2022). The library “hclust” was used to check for collinearity among variables. The models were built under the library “lme4” (Bates et al., 2015).

2.4 Results

A total of 19,632 insects were recorded in our study across the two crops (6,122 in apple sites and 13,510 in oilseed rape sites; Fig.2). Honey bees (*A. mellifera*) were most abundant, accounting for the 72.44% of all individuals recorded (4,270 in the apple sites and 9,951 in the oilseed rape sites; Fig. 2), and hover flies were the second most abundant group in our record, accounting for 8.68% of the individuals (428 in apple sites and 1,276 in oilseed rape sites; Fig. 2). Of the remaining groups of insects recorded, solitary bees contributed to 8.30% of the individuals (612 in apple sites and 1,017 in oilseed rape sites), while bumble bees and butterflies respectively comprised 6.57% and 4.02% of the samples (631 bumble bees in apple sites and 658 in oilseed rape sites; 181 butterflies in apple sites and 608 in oilseed rape sites; Fig.2). Total insect abundances and abundances of all taxonomic groups were significantly higher in oilseed rape sites than in the apple sites (all *P*<0.001; Fig. 2), except for bumble bees (*P*=0.6; Fig. 2).

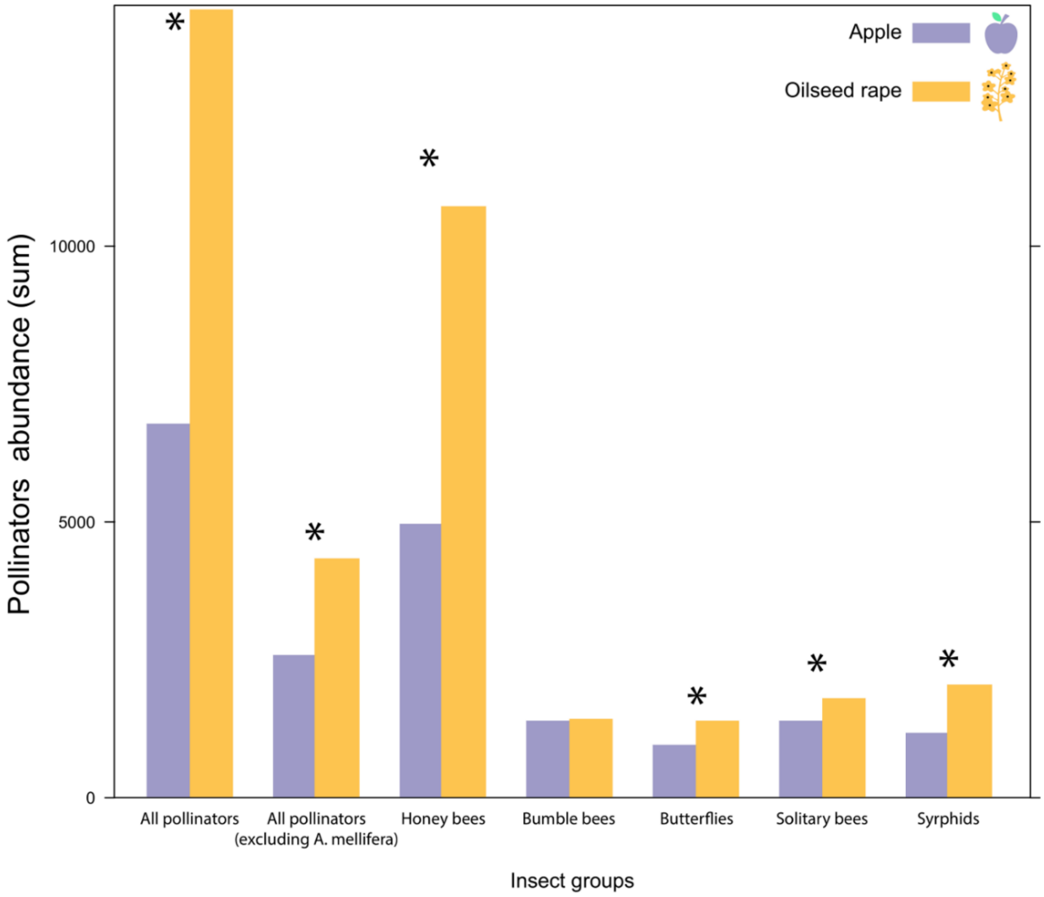

Figure 2. The total number of flower-visiting insects recorded across all sites (All pollinators), excluding honey bees (All pollinators (excluding *A. mellifera*)) and each insect group (*Apis mellifera*, Bumble bees, Butterflies, Solitary bees and Hover flies), according to crop type (purple = apple orchard sites, orange = oilseed rape sites). Asterisks show significant (*P*<0.05) differences between crop types.

2.4.1 Landscape composition

At the field scale, the responses of insects to the number of mass-flowering crops adjacent to the site were taxon-specific (Fig. 3). While bumble bee abundance was positively correlated with the extent of mass-flowering crops and orchards surrounding the apple sites (*P*<0.001; Tabs. 1 and 2; Fig. 3), both honey bees and hover flies recorded in the oilseed rape sites were negatively impacted by their presence (respectively *P*=0.01, and *P*<0.001; Tabs. 1 and 2; Fig. 3). A negative trend emerged also for butterflies in the apple sites, whose abundance showed a moderate decline with the increase of mass-flowering crops and orchards in the surrounding landscape (*P*=0.07; Tabs. 1 and 2).

A higher proportion of orchards in the landscape surrounding the apple sites was negatively correlated with total insect abundance (excluding honey bees; *P*<0.001; Tabs. 1 and 2 and Fig. 3), bumble bees (*P*<0.001; Tabs. 1 and 2) and solitary bees (*P*<0.001; Tabs. 1 and 2). Honey bees were slightly more abundant in sites surrounded by a higher proportion of orchards, although this result was not statistically significant (*P*= 0.08; Tabs. 1 and 2). The proportion of urban area negatively influenced hover flies in the apple sites (*P*=0.02; Tabs. 1 and 2). As expected, a positive relationship between the proportion of less-intensively managed areas and number of flower-visiting insects was found, though the effect was only observed in oilseed rape sites. The total number of insects (excluding honey bees) increased with the increasing proportion of less-intensively managed areas (*P*=0.002; Tabs. 1 and 2; Fig. 3). Similar patterns were observed between the proportion of less-intensively managed areas and the abundance of bumble bees and butterflies (*P*=0.004 and *P*<0.001 respectively; Tabs. 1 and 2).

High landscape diversity in the surrounding landscape increased the abundance of hover flies (*P*=0.02; Tabs. 1 and 2). Solitary bees were also positively influenced by landscape diversity, although this was only found in oilseed rape sites (*P*=0.09; Tabs. 1 and 2).

2.4.2 Landscape configuration

None of the selected explanatory variables describing landscape configuration explained insect abundance, except for habitat isolation (ENN). Contrary to our hypothesis, isolation of less-intensively managed habitat patches was positively correlated with abundance of bumble bees in apple sites (*P*<0.001; Tabs. 1 and 2). On the other hand, isolation of orchard patches was negatively correlated with the abundance of honey bees in apple sites (*P*=0.01 Tabs. 1 and 2). Honey bees in oilseed rape sites showed a positive correlation with the isolation of cropland patches (*P*<0.001; Tabs. 1 and 2). A positive relationship between the isolation of cropland and butterflies was also found in apple sites (*P*<0.001; Tabs. 1 and 2; Fig. 3). However, the opposite was found for butterflies in oilseed rape sites, where abundance declined with increasing isolation of cropland patches (*P*=0.04; Tabs. 1 and 2; Fig. 3).

2.4.3 Weather and climate parameters

Daily temperature, annual temperature, annual precipitation, and precipitation seasonality played a role in shaping insect abundance. Although the positive effect of daily temperature only emerged in oilseed rape sites, annual temperature, annual precipitation and the precipitation seasonality affected insect abundance in both crop types, albeit the effect was positive or negative depending on the insect group and crop type (Tabs.1 and 2; Fig. 3).

The total number of insects in oilseed rape sites was positively correlated with both daily and annual temperatures (both *P*<0.001; Tabs. 1 and 2), but was negatively correlated with annual precipitation (*P*=0.01; Tabs. 1 and 2; Fig. 3). In contrast, annual precipitation had a positive relationship with insect abundance in apple sites, albeit non-significantly (*P*=0.08; Tabs. 1 and 2; Fig. 3).

By analysing the responses of different insect groups to weather and climatic conditions, we found that daily temperature was positively correlated with the number of honey bees, solitary bees and butterflies (respectively *P*=0.003, *P*=0.004, *P*=0.02; Tabs. 1 and 2), while the responses of insects to annual temperature were mostly taxon-specific. The abundance of solitary bees in apple and oilseed rape sites, and hover flies and butterflies in oilseed rape sites were positively correlated with annual temperature (*P*<0.001, *P*<0.001, *P*<0.001 and *P*=0.02; Tabs. 1 and 2), whereas the abundance of bumble bees was negatively correlated with annual temperature in both crop types (*P*<0.001; Tabs. 1 and 2; Fig. 3). Moreover, a positive interaction of annual temperature and landscape diversity on the abundance of solitary bees in oilseed rape sites was found (*P*=0.002; Tab. 1), i.e. that positive effects of landscape diversity were even stronger under warmer climates and *vice versa*.

The effect of annual precipitation on insect abundance varied across crop type and insect group (Tabs. 1 and 2). The abundance of honey bees and solitary bees in apple sites were positively correlated with increasing annual precipitation (*P*< 0.001; Tabs. 1 and 2). On the other hand, solitary bee and butterfly abundances in oilseed rape sites responded negatively to annual precipitation (respectively *P*=0.002 and *P*<0.001; Tabs. 1 and 2). Finally, precipitation seasonality was negatively correlated with the abundance of bumble bees in both apple and oilseed rape sites (*P*<0.001 and *P*=0.02; Tabs. 1 and 2), although it was positively associated with the abundance of honey bees and butterflies in apple sites (*P*<0.001; Tabs. 1 and 2).

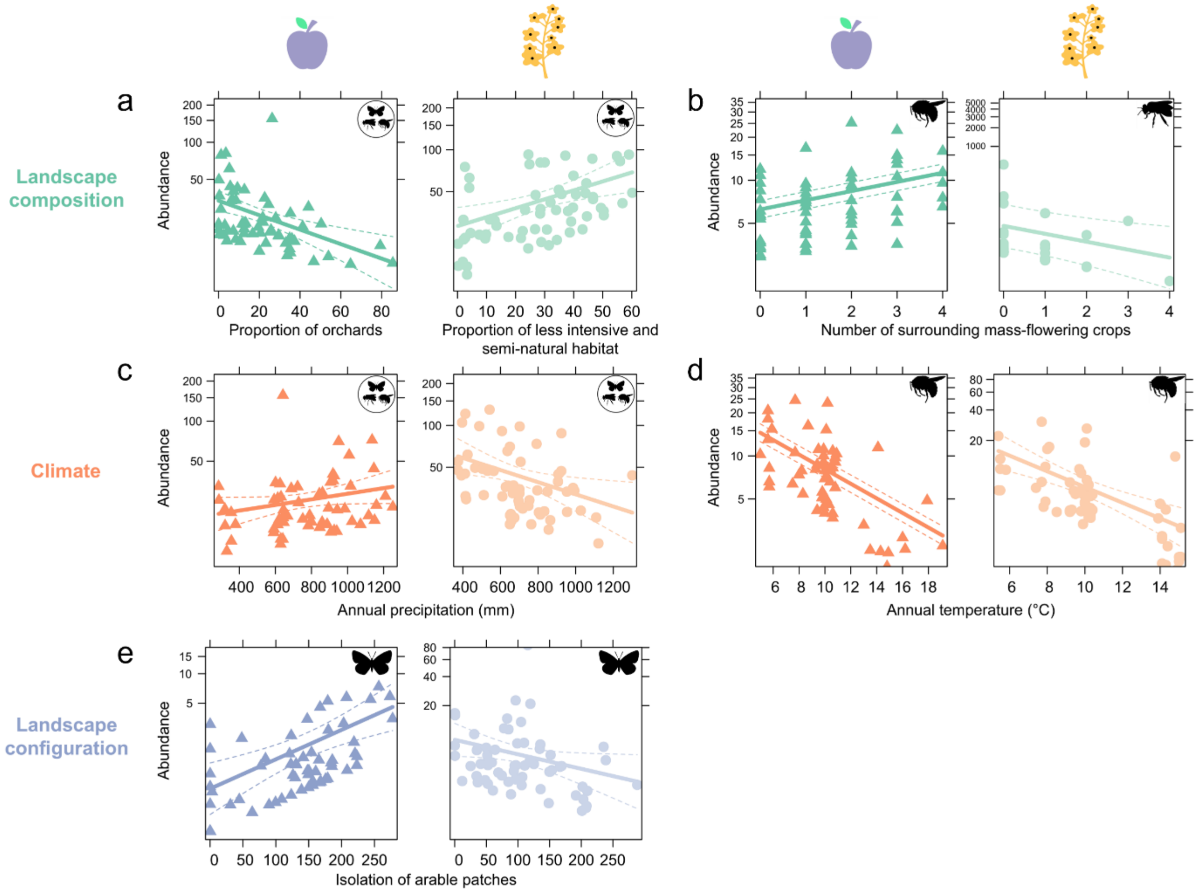

Figure 3. GLMM representing relationships found in both apple and oilseed rape sites between (a) the proportion of orchards or less intensive and semi-natural habitat, and abundance of all pollinators, (b) number of surrounding mass-flowering crops and abundance of bumble bees and honey bees, (c) annual precipitation and abundance of all pollinators, (d) annual temperature and abundance of bumble bees, and (e) isolation of arable patches and abundance of butterflies.

Table 1. The results from the mixed effect models (GLMM models testing the relationship between landscape and climatic variables and insect abundance in each crop – apple (APP) and oilseed rape (OSR). The significant codes are: 0 < *** < 0.001 < ** < 0.01 < * < 0.05 < . < 0.1

Variable	**Crop**	**Insect group**	**Estimate**	**Standard Error**	**Z-Value**	***P*-Value |>Z|**
Orchard Area (%)	APP	All groups	- 0.259	0.071	-3.653	<0.001 ***
		A. mellifera	0.191	0.109	1.748	0.08 .
		Bumble bees	- 0.244	0.003	-81.14	< 0.001 ***
		Solitary bees	- 0.379	0.002	-177.9	< 0.001 ***
Urban Areas (%)	APP	Hover flies	- 0.257	0.112	-2.288	0.02 *
Less-Intensively Managed and Semi-Natural habitats (%)	OSR	All groups	0.2643	0.0873	3.029	0.002 **
		Bumble bees	0.3050	0.1078	2.828	0.005 **
		Butterflies	0.5863	0.1449	4.048	<0.001 ***
Landscape diversity (SHDI)	APP	Hover flies	0.2646	0.1139	2.323	0.02 *
	OSR	Solitary bees	0.2531	0.1504	1.683	0.09 .
Isolation of Orchard Patches	APP	*A. mellifera*	- 0.2430	0.0966	-2.516	0.01 *
Isolation of Cropland Patches	APP	Butterflies	0.5331	0.1412	3.776	<0.001 ***
	OSR	*A. mellifera*	0.3284	0.0909	3.614	<0.001 ***
		Butterflies	- 0.2305	0.1126	-2.047	0.04 *
Isolation of Less-Intensively Managed and Semi-Natural Patches	APP	Bumble bees	0.2756	0.003	91.75	<0.001 ***
Adjacent Mass-Flowering Crops and Orchards	APP	Bumble bees	0.1933	0.003	64.35	<0.001 ***
		Butterflies	- 0.2545	0.1410	-1.804	0.07 .
	OSR	*A.mellifera*	- 0.2341	0.094	-2.491	0.01 *
		Hover flies	- 0.2505	0.0026	-96.536	<0.001 ***
Daily Temperature (º C)	OSR	All groups	0.2197	0.0784	2.802	0.005**
		A. mellifera	0.3516	0.1185	2.966	0.003 **
		Solitary bees	0.4054	0.1417	2.861	0.004 **
		Butterflies	0.2678	0.1164	2.300	0.02 *
Annual Temperature (º C)	APP	Bumble bees	- 0.3429	0.003	-114.10	<0.001 ***
		Solitary bees	0.3331	0.0021	156.6	<0.001 ***
	OSR	All groups	0.2734	0.0808	3.384	<0.001 ***
		Bumble bees	- 0.5060	0.1109	-4.562	<0.001 ***
		Solitary bees	0.6169	0.1480	4.168	<0.001 ***
		Hover flies	0.7222	0.0026	278.230	<0.001 ***
		Butterflies	0.2507	0.1082	2.316	0.02 *
Annual Precipitation	APP	All groups	0.12057	0.06986	1.726	0.08 .
		A. mellifera	0.8155	0.1207	6.754	<0.001 ***
		Solitary bees	0.3548	0.0021	166.7	<0.001 ***
	OSR	All groups	- 0.2046	0.0833	-2.456	0.01 *
		Solitary bees	- 0.4871	0.1563	-3.116	0.002 **
		Butterflies	- 0.5528	0.1257	-4.396	<0.001 ***
Precipitation Seasonality	APP	*A. mellifera*	0.5088	0.124	4.104	<0.001 ***
		Bumble bees	- 0.2362	0.003	-78.64	<0.001 ***
		Butterflies	0.8481	0.1454	5.832	<0.001 ***
	OSR	Bumble bees	- 0.2387	0.1047	-2.279	0.02 *
Annual Temperature (º C) * Landscape diversity (SHDI)	OSR	Solitary bees	0.4247	0.1345	3.157	0.002 **

Table 2. Summary of the positive ("+") and negative ("–") effects of landscape and climate variables on the abundance of the six groups of pollinators. The first column shows the different pollinators groups (All pollinators, excluding honey bees; Honey bees; Bumble bees; Solitary bees; Hover flies; and Butterflies). The upper part of the table shows the interactions found in the apple sites, while the bottom part the ones in the oilseed rape crops. Orchards (%) = proportion of orchards; Urban (%) = proportion of urban areas; Less intensive & SNH (%) = proportion of less-intensively managed and semi-natural areas; SHDI = landscape diversity; MFC = number of mass-flowering crops and orchards; ENN Orchards = isolation of orchard patches; ENN Less intensive & SNH = isolation of less-intensively managed and semi-natural; ENN Arable =isolation of cropland patches; ; Daily T °C = daily temperature (temperature recorded at the moment of the sampling); Annual T °C = annual temperature; Annual Precipitation; and Precipitation Seasonality. Only significant relationships (p-value < 0.05; in black) and those representing a trend (0.05 < p-value < 0.1; in grey) are shown in the table.

		Orchards (%)	Urban (%)	Less intensive & SNH (%)	SHDI	MFC	ENN Orchards	ENN Less intensive & SNH	ENN Arable	Daily T °C	Annual T °C	Annual precipitation	Precipitation seasonality
	All taxa	−										+	
	Honey bees	+					−					+	+
	Bumble bees	−				+		+			−		−
	Solitary bees	−									+	+	
	Syrphids		−		+								
	Butterflies					−			+				
	All taxa			+						+	+	−	
	Honey bees					−			+	+			
	Bumble bees			+							−		−
	Solitary bees				+					+	+	−	
	Syrphids					−					+		
	Butterflies			+					−	+	+	−	

2.5 Discussion

2.5.1 Impact of landscape composition and configuration on insect abundance

Our results demonstrate that both the composition and configuration of the landscape, such as landscape diversity, the presence of less-intensively managed land, but also the complexity and connectivity of the landscape, were major drivers of flower-visiting insect abundances in agriculturally dominated landscapes. As expected, a higher proportion of less-intensively managed habitats was found to support higher numbers of flower-visiting insects. However, we found these effects to be highly context dependent, in regard to both taxon and crop-type. Because we used a non-destructive sampling method (Hodge et al., 2022), we considered insect abundance in very broad taxonomic categories in our analyses. While previous studies found responses to surrounding habitat structure can vary within these broad groups, probably due to scale-dependent ecological requirements of species, particularly within the species rich groups of hoverflies and solitary bees (Stanley et al., 2013), we were not able to investigate species-level patterns.

In addition, differences related to crop-type emerged in relation to insect abundance, with more individuals recorded in oilseed rape crops, compared to apple orchards – with the exception of bumble bees. Oilseed rape crops are known to be highly attractive to bees, and the pollen diet of some species (e.g. honey bees and red mason bees) consists predominantly of mass flowering crops when available (Holzschuh et al., 2013; Stanley & Stout, 2013). However, bumble bees also include other species in their diet, even when mass-flowering crops are abundant (Kovács-Hostyánszki et al., 2013). Similarly, apples are pollinator-dependent, attracting a wide diversity of insects (Russo et al., 2015; Gamonal Gomez et al., 2023; Burns et al., 2022). However, their nectar production is lower compared to oilseed rape flowers, and some groups of insects (i.e. honey bees) have been shown to be attracted away from apple orchards, when oilseed rape crops were co-occurring in the vicinity (Quinet et al., 2016; Carruthers et al., 2017; Osterman et al., 2021). On the other hand, oilseed rape crops can attract some insects species from the surrounding landscape, given their abundant flower resources and theur flower density (Hoyle et al., 2007; Vrdoljak et al., 2016; Magrach et al., 2017; Rollin et al., 2013; Van Reeth et al., 2018; Woodcock et al., 2016). Another explanation for the different number of insects recorded in the two crops could be related to management. Previous studies showed that apple orchards were associated with high level of pesticides (with fungicide contributing to over the 98% of the total pesticides residues in pollen collected by bees; Šlachta et al., 2020). Although generally not toxic to bees (Rondeau & Raine, 2022), some fungicides can negatively impact the behaviour and fitness of honey bees (Liao et al., 2019; European Commission Implementing Regulation EU 2018/1865 of 28 November 2018). In addition, despite the pollen and nectar resources offered by the target crops during sampling, some pollinator groups might have been attracted to the target crops by other species of plants growing within and along the margins of the fields. These non-crop plants may themselves differ between as a result of fundamental differences in cultivation; oilseed rape is an annual field crop and apples a woody orchard crop. In fact, previous studies show that some insect groups are more abundant along the margins of the cultivation rather than in the centre of the crop itself (e.g. butterflies and hover flies; Bottero et al., 2021). Similarly, the larvae of butterflies and some hover fly species feed on plant tissues (particularly the larvae of *Pieris* butterfly species that favour Brassicacea), whilst other hover fly larvae are saprophagous or predatory (Speight et al., 2010). Thus butterfly and hover fly abundance in crops may be determined by factors other than the availability of floral resources.

2.5.1.1 Less-intensively managed habitats

Our results show that the abundance of different groups of pollinators increased with the proportion of less-intensively managed habitats and with habitat diversity, confirming that heterogeneous habitats can support beneficial insects in agricultural landscapes, likely by offering a greater diversity of food and resources (Marini et al., 2012; Martínez-Núñez et al., 2022; Nayak et al., 2015; Raderschall et al., 2021; Rundlöf et al., 2008). Different pollinator taxa have different ecological and physiological requirements, and even individuals of the same species might benefit from diets based on a diversity of plant species (Bertrand et al., 2019; Cane & Sipes, 2007; Eckhardt et al., 2014), and during different stages of their life cycle (Erhardt, 1985; Erhardt & Mevi-Schütz, 2009; Meyer et al., 2009). Therefore, less-intensively managed and semi-natural habitats might fill nutritional gaps at specific times of the year, such as at the end of the abundant, yet temporally constrained flowering period of mass-flowering crops (Bottero et al., 2021; Timberlake et al., 2019). The less-intensively managed habitats in the landscape surrounding the fields, may also play an important role in promoting pollinators. For instance, Maurer et al. (2022) reported that different types of semi-natural features (meadows, floral strips in the cultivated crops, hedgerows) have a different impact on the richness and the abundance of different flower-visiting insects, depending on the insects' needs and the time of year they are active. Similarly, the presence of floral strips in cultivated crops promoted bumble bees across seasons (Bommarco et al., 2021), while hover flies and butterflies were shown to favour the crops' flowering margins (Bottero et al., 2021). Similarly, the diversity and growth stages of the plants present in the floral strips can support pollinator communities in cultivated crops, ultimately promoting pollination services in agricultural landscapes (Albrecht et al, 2020). In addition, Raderschall et al. (2021) showed that higher crop diversity (and semi-natural habitats) may support bumble bee density in agricultural landscape.

2.5.1.2 Highly managed crop and urban habitats

Urban areas and highly managed crops such as orchards decreased the abundance of different groups of flower-visiting insects. The negative impact of anthropogenic habitats on insect communities is likely to be related to habitat disturbance and/or management intensity (McKinney, 2008; Vanbergen, 2013). An increase in the proportion of both cropland and orchards adds to the overall intensification burden throughout the landscape, through agrochemical inputs and reduced nesting opportunities, not only in the actual cropland fields and orchards, but also outside of these, due to crop rotation and the persistence and dispersal of agrochemicals through soil and groundwater to areas beyond their initial application.

Apple orchards are usually subjected to intensive application of plant protection products to maximize crop value (Damos et al., 2015). As a result, they may directly lead to declines in pollinator abundance, or precipitate their departure from target crop sites to the surrounding areas – the latter may be particularly true for honeybees and bumble bees, which are known for their long foraging distances (Beekman & Ratnieks, 2000; Carvell et al., 2012; Knight et al., 2005). Many of the adjacent patches in our apple sites were mass-flowering crops, including oilseed rape and other orchards, which may have caused a dilution of flower-visiting pollinators for high floral rewards in the vicinity, especially when these mass-flowering crops bloom at the same time (Bänsch et al., 2021; Grab et al., 2017; Holzschuh et al., 2016; Osterman et al., 2021; Riedinger et al., 2015; Stanley & Stout, 2013). However, in contrast to our results, Osterman et al., (2021) did not observe a shift in bumble bee abundance when apple sites were surrounded by oilseed rape, but found more solitary bees in apple sites. These differences could be explained by the different types of crops surrounding our sites, though we do not have the necessary information regarding the cultivar nor the intensity of inputs used in the surrounding crops.

2.5.1.3 Mass-flowering crops and orchards adjacent to the sites

Competition for better floral rewards between different crop types may also explain the negative relationships found between the abundance of honey bees and hover flies, and the presence of mass-flowering crops and orchards in the adjacent patches. The proximity of mass-flowering crops and orchards in the vicinity could lead to the dilution of pollinators (Robinson et al., 2022). Alternatively, low plant richness in mass-flowering monocultures may explain the low abundance of pollinators found in mass-flowering dominated landscapes. Indeed, butterflies, bees and hover flies require different plants to properly complete their life cycle (Erhardt, 1985; Erhardt & Mevi-Schütz, 2009), and thus can strongly benefit from the presence of semi-natural habitats that offer a greater diversity of floral resources (Nayak et al., 2015; Rundlöf et al., 2008; Steffan-Dewenter et al., 2002). On the other hand, bumble bees seemed to profit from the presence of mass-flowering crops in the vicinity, likely due to their longer foraging ranges combined with the highly attractive nature of these crops, which corroborates the findings of previous studies (Holzschuh et al., 2013; Stanley & Stout, 2013).

2.5.1.4 Habitat configuration

Although the spatial arrangement of crop fields and other habitats has been shown to promote insects in agroecosystems (Martin et al., 2019), habitat isolation was the only configurational landscape metric that influenced the abundance of flower-visiting insects. The effects of habitat isolation on pollinators in our study sites appeared to be highly context dependent. In oilseed rape fields, more honey bees were found when the nearest croplands were further away, as opposed to butterflies which were more abundant when croplands were close by. We found the opposite trend in apple sites, where more honey bees were found when the nearest orchard was close, and more butterflies when the nearest cropland was further away. Contrary to our expectations (Fahrig, 2013; Perović et al., 2015), we found more bumble bees in apple sites when the less-intensively managed habitat patches were further away.

The opposing trends observed for honey bees and butterflies may be due to the differences in their foraging behaviour and ranges, the composition of the landscape surrounding the sites, and the crop’s attractiveness in regards to flower rewards. Honey bees can forage over large distances, and are known to be central-place foragers that recruit individuals to more rewarding patches (Seeley 1995; Dyer 2002). The placement of honey bee hives is usually managed by beekeepers to optimize both access and proximity to a diversity of high-yielding floral resources, especially in highly managed crops such as apple orchards. Thus, the high number of honey bees found in our apple sites may be explained by the presence of numerous honey bee hives manged by beekeepers, especially since many other orchards were found in the vicinity. Butterflies on the other hand are part of a much more diverse group that is influenced by a number of factors mostly related to foraging behaviour, mating opportunities and oviposition resources at the patch and landscape level (Dover & Settele, 2008). Butterflies generally benefited from the isolation of the cropland in apple sites, suggesting that cropland offered poor rewards to butterflies, as opposed to less-intensively managed habitats. Similarly, we did not assess overall crop diversity and thus lack the information about specific crops in the vicinity of oilseed rape and apple sites. Although honey bees seem to favour oilseed rape sites that are further away from croplands, we can only presume that our oilseed rape sites were in landscape dominated by less attractive crops for honey bees, e.g. cereal fields. In contrast, oilseed rape fields may need to be less-isolated to attract butterflies, suggesting that the temporary boost of early floral resource pulse provided by mass-flowering crops are not sufficient to support butterflies in more intensive landscapes.

2.5.2 Impact of weather and climate variables on flower-visiting insects

In the context of general concern about the impact that heat waves, droughts, and changes in temporal dynamics (including precipitation seasonality) can have on flower-visiting insects, our study collected important information about the responses of different groups of pollinators at a European level, albeit the relationships were highly context dependent.

As expected, the abundance of several taxa of flower-visiting insects decreased with increasing annual precipitation and precipitation seasonality. On the other hand, only bumble bees responded negatively to annual temperature.

2.5.2.1 Daily and annual temperature

Our results showed that both daily and annual temperatures positively influenced the abundance of most of the studied insect groups, as could be expected given that most insects are ectotherms and more active during warmer day periods. Fewer bumble bees were found when annual temperatures were higher though; as temperate species, they are generally more suited to northern latitudes in Europe and lower temperatures (Rasmont and Iserbyt, 2014). Changes in temperature, especially when rising above specific levels and during the developmental stages of the species, can negatively affect flower-visiting insects by impacting foraging activities, fertility, morphology (wing and tongue length and body size), colony productivity and development time, and survival (Gerard et al., 2018a; Gerard et al., 2018b; Holland & Bourke, 2015; Martinet et al., 2021; Miller-Struttmann et al., 2015; O’Neill et al., 2011; Radmacher & Strohm, 2010; Tepedino & Parker, 1986; Weidenmüller et al., 2002). Moreover, higher temperatures are linked to earlier emergence of flower-visiting insects, which can have repercussions on plant-pollinators interactions (Hegland et al., 2009). Furthermore, higher temperatures are often related to drought, extreme weather phenomena, and to changes in seasonality with possible adverse consequences on plant communities and the resulting cascading effects on food resources (Lawson & Rands, 2019; Höfer et al., 2021). In the face of climate change, a better understanding of the relationships between pollinator abundance and temperature is crucial, given the risk that higher temperatures may result in more homogeneous pollinator communities, likely associated with higher dispersion rates, with a consequent decrease of the species pool (Ganuza et al., 2022).

2.5.2.2 Annual precipitation and Precipitation Seasonality

Precipitation can directly affect insects, e.g. their flight mechanism and sensory signals, but also indirectly affect their food resources (Lawson & Rands, 2019). It is also responsible for nectar dilution and pollen damage in some plant species, but the corolla shape and the position of nectaries, nectar spurs and anthers can facilitate the protection of pollen and nectar from rain or drought (Lawson & Rands, 2019). Although both apple and oilseed rape flowers are characterised by an open corolla, we found contrasting responses of insects to annual precipitation in both crop types, suggesting that the differences in landscape composition and configuration, rather than direct impacts of precipitation on food resources, are more important in shaping pollinator communities. Apple sites were surrounded by a higher proportion of both diverse and less-intensively managed habitats, and associated with a lower isolation between semi-natural patches. Such landscape structures might facilitate access to different flower resources, e.g. when pollen was damaged, or when the nectar of the mass-flowering crops was diluted. The contrasting effects of precipitation on different taxonomic groups might be explained by morphological differences in body size and wing structure of the different taxa (Lawson & Rands, 2019), or indirectly mediated through forage resources. Flowers pollinated by butterflies usually have more dilute nectar, while bee-pollinated ones show higher sugar concentrations (Lawson & Rands, 2019; Pyke & Waser, 1981; Baker and Baker 1983), suggesting that the different responses to the precipitation seasonality on butterflies might be related to taxa preferences for nectar resources. However, changes in floral communities related to different climate event may also be responsible for a shift in flower-visiting insect community.

2.5.3 Conclusion

The adoption of a standardized insect sampling protocol across 128 structurally different sites characterised by different climatic and weather conditions, and the decision to focus on multiple groups of insects, allowed us to properly account for context dependency when disentangling the effects of landscape heterogeneity and climate on pollinator communities at a European level. Despite being constrained to a single flowering season, and due to logistical constraints in conducting the study at the European scale, our study offers important insights on the combined effects that climate and landscape structure have on flower-visiting insect communities. Overall, our results indicate that heterogeneous landscapes, characterised by diverse and less-intensively managed habitats, with low levels of patch isolation, can have a positive impact on the communities of flower-visiting insects, even when the landscape is dominated by intensive agricultural land use. Conversely, structurally simple landscapes will likely be associated with a loss of flower-visiting insects (Senapathi et al., 2017).

Moreover, our study offers new evidence about the importance of both weather and climate parameters on shaping flower-visiting insect communities across Europe. This is particularly relevant in the context of climate change, which will have direct or indirect repercussions on insects and plants communities in the next few decades. Furthermore, due to the strong impact of climate on pollinators shown in this study, we recommend including weather and climate parameters in studies investigating pollinator communities, notably in regard to different biogeographic ranges and fluctuating weather patterns. Additionally, future studies that aim to generate a better understanding of the impact of landscape configuration on insect population dynamics should also focus on the natural structural elements present in the landscape, which have previously been shown to play a major role in influencing insects, especially in an intensive agricultural context (Dover & Sparks, 2000; Cranmer et al., 2012; Marshall & Moonen, 2002).

Broadly, our take-home message is that despite some taxonomic variation, landscape simplification negatively affects some important pollinating insect taxa. Taken with other studies, which have reported similar findings for other taxonomic groups, there may be widespread implications of landscape simplification on multifunctionality and the delivery of multiple ecosystem services (Dainese et al. 2017; Martin et al. 2019; Le Provost et al. 2021). Together, these findings support the implementation of land-use plans and policies to preserve heterogeneity and semi-natural features at a field and landscape level in Europe, to sustain the communities of beneficial insects in agricultural landscapes. For example, increasing the amount of less-intensively managed and semi-natural habitats in landscapes characterised by oilseed rape cultivation, could promote pollinator abundance in oilseed rape crops. On the other hand, in habitats dominated by apple orchards, decreasing the total orchard area, and/or increasing crop diversity and the number of types of mass-flowering crop, could have a positive impact on pollinating insect communities.

As well as helping to reverse decline and restore pollinator populations, which are key global and European biodiversity targets, this could have knock-on benefits for other taxa and the restoration of biodiversity more broadly in agriculturally-dominated landscapes across Europe.

2.6 Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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CHAPTER 3

Taxon-specific temporal shift in pollinating insects in mass-flowering crop and field margins in Ireland

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3.1 Abstract

In intensively cropped agricultural landscapes, the vegetation in edges and hedges (henceforth "field margins") represents an important semi-natural habitat providing fundamental resources for insect pollinators. We surveyed the pollinating insects associated with two mass-flowering crops, apple and oilseed rape, and compared the insect fauna of the main crop with that in the field margins in the grass-dominated agricultural landscapes of Ireland. Different insect groups responded differently to the presence of the flowering crop, with honey and bumble bees more abundant in crops than margins during crop flowering, but more hover flies and butterflies in margins throughout. The composition of the insect assemblage also shifted over time due to taxon-specific changes in abundance. For example, solitary bees were most abundant early in the season, whereas hover flies peaked, and butterflies declined, in mid-summer. The temporal shift in insect community structure was associated with parallel changes in the field margin flora, and, although we found no relationship between insect abundance and abundance of field margin flowers, *Bombus* abundance and total insect abundance were positively correlated with floral diversity. After the crop flowering period, floral abundance and diversity was maintained via margin plants, but by late summer, floral resources declined. Our results confirm the importance of field margins for insect pollinators of entomophilous crops set within grass-dominated landscapes, even during the crop flowering period, and provide additional support for agri-environment schemes that protect and/or improve field margin biodiversity. The results also demonstrate that although shifts in insect and plant communities may be linked phenologically there may not always be simple relationships between insect and floral abundance and richness.

Key words: *Apis mellifera*, *Bombus* spp., hover flies, butterflies, Ireland, phenology

3.2 Introduction

Flower-visiting insects such as honey bees, bumble bees, solitary bees, hover flies and butterflies provide an ecosystem service by pollinating a wide range of wild and cultivated plants (Ollerton et al. 2011). Many of these insects are declining due to a combination of threats arising from habitat loss, pesticide exposure, invasive species and climate change (IPBES 2016). Habitat disturbance (fragmentation, degradation and habitat loss) is one of the main stressors negatively impacting insect communities (Goulson et al. 2008; Winfree et al. 2009; Le Féon et al. 2010; Kovács-Hostyánszki et al. 2011; Scheper et al. 2013; Hass et al. 2018), with associated losses of floral resources subsequently leading to disruption of plant-pollinator interaction networks (Day 1991; O' Toole 1994; Gathmann & Tscharntke 2002).

Shifts in land use from semi-natural habitat to intensive agriculture have been associated with greatly reduced biodiversity, including pollinating insects, in many regions of the world (Ghazoul 2005; Goulson et al. 2008). In degraded agricultural landscapes, outside of the flowering period of mass-flowering crops, both managed and naturally-occurring pollinating insects can face 'hunger gaps' when the quantity and quality of pollen and nectar available does not meet requirements (Timberlake et al. 2019). In this scenario, hedgerows and naturally-occurring wild flowering species in field margins represent an important food resource for many insect species (Stanley & Stout 2014), and positive relationships between farmland pollinating insects and the diversity of floral resources in these habitats are often demonstrated (e.g. Papanikolaou et al. 2017). In addition, hedgerows and field edges (i.e. the space beyond the edge of the crop, and the physical boundary, be that a wall, hedgerow or fence; henceforth "field margins") provide shelter, larval host plants, a source of prey, and relatively high floral diversity compared with that occurring in the centre of the main crop, and so are important for supporting biodiversity in agricultural landscapes (Wratten 1988; Marshall & Moonen 2002). Because of their natural seasonal flowering sequence, the plants in field margins provide resources at different times of the year, at different stages of the pollinator life cycle, and/ or the development of the colony (Rotenberry 1990; Marshall & Moonen 2002; Cole et al. 2017). Additionally, the interactions between managed and wild pollinators will, inevitably, change in space and time in relation to both the phenologies of the mass-flowering crop and that of the wild plant species present in the same foraging ranges.

Deliberate introduction of native plant species into field margins, augmentation of flora by sowing seed mixes or the creation of floral 'strips', are common techniques used in agri-environment schemes to increase numbers and diversity of pollinators and other beneficial insects (e.g. Haaland et al. 2011; Campbell et al. 2017; Curtis et al. 2019; Heller et al. 2019). The value of these planting schemes to pollinating insects, however, can be highly variable and taxonomically biased (Campbell et al. 2017; Wix et al. 2019), and their overall effectiveness can be dependent upon the landscape context and the type of farming under consideration (e.g. cropland vs grassland)

(Scheper et al. 2013). In general, studies have focussed on the role of field margins for pollinators in crop-dominated landscapes, and in grasslands of "high biological value" – e.g. wet, calcareous or alpine grasslands (Marshall & Moonen 2002; Plantureux et al. 2005). Relatively few studies have examined the role of field margins in shaping insect communities in agricultural landscapes dominated by intensive grasslands (but see Power & Stout 2011; Stanley & Stout 2013).

In the Republic of Ireland, more than 60% of total land area is managed as agricultural land, and 80% of this land is considered as "improved" (i.e. intensively managed) agricultural grassland for livestock production and dairy, with a smaller area used for arable-based crop and horticultural production (The Heritage Council, 2010; Marshall & Moonen 2002; Sheridan et al. 2011; Scheper et al. 2013). These landscapes are characterised by highly modified monoculture grasslands and rye-grass leys, subjected to intensive management, such as reseeding, fertilisation, grazing and silage making (Fossitt 2000). Field margin structures such as hedgerows are a consistent feature in Irish farmland, and in a landscape dominated by species-poor improved grasslands, often provide a large portion of the semi-natural habitat available for wild pollinators and other wild animals. Larkin et al. (2019), in a study of 119 intensively managed farms, reported that hedgerows were present in 100% of arable, beef and dairy farms and comprised almost 3% of their areas.

Flowering crops are rare in Irish landscapes but include oilseed rape (OSR; ~ 10,000 ha grown in Ireland), other brassicas used for animal fodder, and apples for both direct consumption and cider making (~ 700 ha; fao.org/faostat 2018 data). As mass-flowering entomophilous crops, both apples and OSR produce large amounts of pollen and nectar that attract a range of flower-visiting insects, and are especially useful for insects such as bees when high quantities of resources are required early in the season for nest establishment and, in social species, colony growth. In terms of pollination services, apple growers often augment natural pollinator populations by installing commercially produced bumble bee colonies and/ or have honey bee apiaries onsite. Oilseed rape is not obligately dependent on bees or other insects for pollination, but beekeepers often site apiaries on or near OSR fields, and studies have shown that seed set and total yield can be significantly reduced if insect pollinators are excluded (Stanley et al. 2013; Perrot et al. 2018).

Thus, overall, communities of pollinating insects in field margins will be influenced by multiple factors, including landscape context, crop type and management, the diversity and abundance of flower resources present in the field margin and seasonality with regards to crop mass-flowering. This study used both an annual (OSR) and a perennial (apple) early-season, mass-flowering crop, within a grass-dominated agricultural landscape, to: (1) compare the abundance of major pollinating insect groups within the centre of the main flowering crop with their abundance in the field margins, (2) investigate whether and how the composition of the pollinator assemblage shifted in time, in connection with the changes that occur during and after the blossoming period of the mass-flowering crops, and (3) identify any relationships between insect abundance and diversity with the abundance and diversity of wild flowering plants occurring in field margins.

3.3 Methods

3.3.1 Study sites

The investigation was conducted between April and August 2019 at eleven study sites in The Republic of Ireland. Six sites consisted of fields of winter-sown OSR to represent an annual mass-flowering crop, and five sites were apple orchards that represented a perennial flowering crop (Fig. 4; Appendix IV). Study sites ranged in size from 0.4 ha to 22 ha and were a minimum distance of 9 km apart. The area of grassland in the landscape which surrounded the sites (1 km radius) ranged approximately from 15% to 74%, with a mean of almost 40% (Appendix IV). All sites had honey bee hives (≥ 3) and commercial colonies of *Bombus terrestris* (≥ 3) along some field boundary or in close proximity.

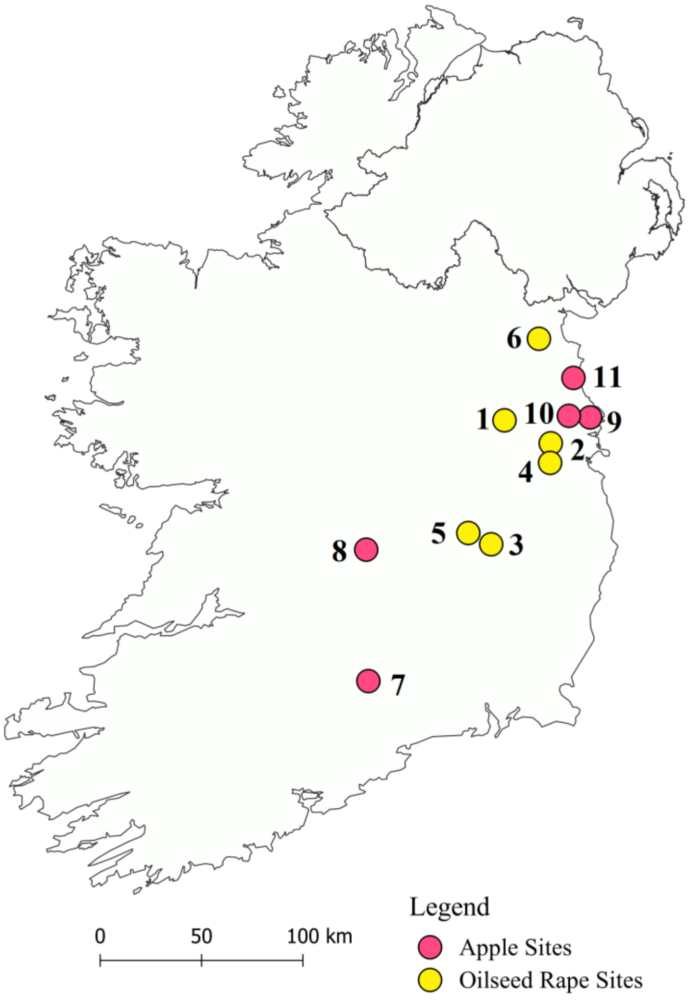

Figure 4. Location of study sites. Numbers correspond with descriptions in Appendix I. *Image created with QGIS software.*

3.3.2 Insect surveys

The aims of the insect pollinator surveys were twofold: (1) to compare the communities of insects within the centre of the target crops with their associated field margins during the crop flowering period, and (2) to examine how the field margin insect communities changed over time relative to the flowering period of the main crop.

Each survey consisted of walking a 100 m transect over a 10-minute period and recording the flower-visiting insects 1 m either side of the observer (total area 200 m2), both those actually visiting flowers, and those flying/resting in the transect area. Effort was made to avoid re-counting the same individuals during the course of the surveys but, since individuals were not captured, it is possible that some individuals were counted more than once. All surveys were performed between 9 am and 6 pm and were conducted during suitable weather conditions for insect activity (wind speed < 6 m/s; temperature 10-28°C; no rain).

For quantitative analysis, insects were assigned to one of five groups: *Apis mellifera*, *Bombus* spp, solitary bees, hover flies, or butterflies. We chose to use these five pollinator taxa because they are well recognized, sub-divisions of the pollinating insects, and we feel information at this level provides a suitable description of the coarse structure of the functional guild. We did not perform any lethal sampling which meant that we could not identify hoverflies and solitary bees to species with confidence. Nevertheless, to gain some insight into which species were found in the study sites, the more abundant butterflies and *Bombus* were also identified to species level, with cryptic *Bombus* species grouped under the label of *Bombus terrestris*/*lucorum* agg.(Carolan et al. 2012).

As a measure of insect richness, the number of insect groups (from five) present in each site visit was recorded. The counts of each of the five groups were then used to produce a version of the Shannon-Wiener diversity index, where diversity (H) = $-\Sigma pi.\ln(pi)$ and pi is the proportion of individuals making up the *i*th insect group.

The pollinator surveys were performed during three different periods (Appendix IV):

1. During the crop flowering period (April-May 2019)

2. Approximately one to two months after the crop flowering period (June-July 2019)

3. Approximately three months after the crop flowering period (August 2019)

In Period 1, during crop flowering, each site was visited on two occasions. On each visit, two 10-minute insect surveys were performed in the centre of the crop, and then a mean of the counts for each insect group obtained. The two transects were chosen to be at least 30 m apart. The samplings were performed close to the crop centre or, when the crops/orchards were too wide, at least 30m from the edge of the crop. Similarly, two 10-minute surveys were performed in the field margins (one survey on each of two randomly chosen field boundaries) and a mean of these counts was obtained.

To examine the change in field margin insect communities over time, each site was visited on two occasions in Periods 2 and 3. At all 11 sites, one 10-minute field margin survey was performed on each of two randomly chosen field boundaries on each visit. For each site, the pollinator counts on each sampling visit were performed on the same two margins that were randomly chosen during Period 1. Additionally, at the apple sites, two 10-minute insect surveys were also performed in the centre of the crop. No surveys were performed in Periods 2 and 3 in the centre of OSR crops because of limited access to the fields due to normal farming operations.

3.3.3 Survey of flowering plants

The aims of the floral surveys was to collect information concerning the relative abundance and diversity of floral resources in addition to the main crop during the different periods of the study. One floral survey was conducted at each site in each study period.

In each survey, the field margin flora was assessed at 12 locations, located at approximately 25%, 50% and 75% of the length of the four main field boundaries. GPS coordinates of each location were recorded so approximately the same locations could be used in each study period. Using a 1 x 1 m quadrat to give a standardized sample area, at each location, the entomophilous plant species that were in flower were recorded on the ground and also in a vertical plane at a height of 1.5 m if the boundary was surrounded by a hedge, wall or fence. In each quadrat, the total number of floral units (Dicks et al. 2002; Baldock et al. 2015) present was assigned to four categories: 0 ≡ no flowers present; 1 ≡ 1-10 floral units; 2 ≡ 11-100 floral units; 3 ≡ > 100 floral units.

To produce a summary measure of floral abundance on each site visit, the median of the 12 scores was calculated. As a measure of floral diversity, the number of flowering species present in the 12 samples, on each site visit, was recorded. Additionally, we thought it desirable to include a diversity index in addition to floral species richness to provide additional information on the evenness (or dominance) of the flowering plants present at each site. Rather than abundance of floral units, we have used the presence of each plant species in each of the 12 quadrats to reflect their frequency in the overall assemblage. We then used a version of the Shannon-Wiener diversity index calculated as, $H = -\Sigma fi.\ln(fi)$, where fi is the frequency of the ith species in terms of the proportion of sampling locations (from 12) where it was recorded.

3.3.4 Data analysis

Statistical analyses were performed using Genstat v19 software (VSN International Ltd UK) and Community Analysis Package v4 (Pisces Conservation Ltd., UK). [1]

During the crop flowering period, to compare the insects present in the crop centre with those found in the field margins, account had to be taken of the non-independence of comparisons made within each site, and on each sampling visit. Therefore, a residual maximum likelihood (REML) mixed model was fitted with crop type (APP or OSR) and location (crop centre or field boundary) defined as fixed factors and site and sampling visit as random factors. To compare the insect assemblages in the centre and field margins of the apple crops over the three sampling periods, a REML repeated-measures model was fitted with location (crop centre or field margin) and sample period treated as fixed factors and site and site-visit as random factors.

For the analysis of the field margin insect and floral data (abundance, species richness and diversity) over time in both crops, a REML repeated-measures model was fitted with crop type (APP or OSR) and sample period fitted as fixed factors and site as a random factor. For this analysis, a mean of the insect counts from all four surveys over the two visits for each site was obtained, resulting in one value per site per period for each pollinator group. This procedure simplified the repeated measures analysis, and resulted in an insect taxon-by-sample matrix with the same structure as that of the floral taxon-by-sample matrix, which subsequently allowed the comparison of insect and floral similarity matrices using a Mantel test (as described below). In the above REML analyses, insect counts were square root transformed prior to analysis, to lessen the effects of extreme counts and increase normality of error terms. Insect taxonomic richness and diversity and all three of the floral response variables were not transformed.

Examination of the relationships between field margin insect abundance and diversity with floral abundance and diversity were assessed by Spearman's rank correlation using the summary data from the 33 site visits.

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[1] Alternative analyses were repeated in R studio (version 22.07.1). The analyses description and results can be found in the Appendices V, VI, VII, VIII, IX.

To examine the composition of the field margin insect and floral assemblages present in each crop in each period, non-metric multidimensional scaling (NMDS) was performed based on Bray-Curtis similarity matrices. For the analysis of floral data, the frequency of each species, from 12 positions around the field boundary, was used as a measure of relative abundance. For the insects, the square root of the mean counts for each taxon at each site in each time period were used in the analysis. Separation of samples based on crop and sampling period was assessed using analysis of similarity (ANOSIM; Clarke 1993; Henderson & Seaby 2008), which produces an indication of statistical significance by comparing the relative within- and between-group similarity with that obtained by 1000 random permutations of the raw data.

A Mantel test, based on the similarity matrices used for the NMDS, was used to examine the association between the shifts in the plant and field margin insect assemblages over time and between crop types. This test used Spearman's rank correlation to give a base indication of the strength of the relationship and obtained a P-value by calculating the proportion of 1000 random permutations of the similarity matrices which produced a higher correlation coefficient. The whole process was performed 20 times and a mean P-value obtained.

3.4 Results

A total of 3,048 insect was recorded during the 216 ten-minute surveys (36 hours of observation) carried out during the whole study, consisting of 1,052 *Apis mellifera*, 618 *Bombus* spp., 167 butterflies, 1,013 hover flies and 198 solitary bees.

3.4.1 Insects in the crop centre and field margins during the crop flowering period

In the 88 ten-minute surveys (total 14.67 hours of observations) carried out during the main crop flowering period, a total of 1,543 pollinating insects were observed, consisting of 900 *Apis mellifera*, 264 *Bombus* spp., 150 solitary bees, 174 syrphids and 55 butterflies. There were no overall statistically significant differences between the apple and OSR crops in terms of insect diversity or the abundance of any of the five insect groups, although there was moderate evidence ($P = 0.055$) that solitary bees were more abundant in apples than OSR (Tab. 3A; Fig. 5).

Apis mellifera and solitary bees showed no significant differences in abundance between the crop centre and the field margins (Tab. 3A; Fig. 5), whereas butterflies and syrphids were more abundant in the field margins than in the crop centre, especially in OSR. *Bombus* were more abundant in the crop centre than in the field margins, although this effect was only apparent in the apple orchards (Fig. 5, Appendix X). The most abundant butterfly species recorded were *Anthocaris cardamine* and *Pieris* spp. (Appendix X). Five species of *Bombus* were recorded: *B. hortorum*, *B. pascuorum*, *B. pratorum*, *B. lapidarius* and individuals belonging to the *B. terrestris*/*lucorum* aggregation (Appendix X).

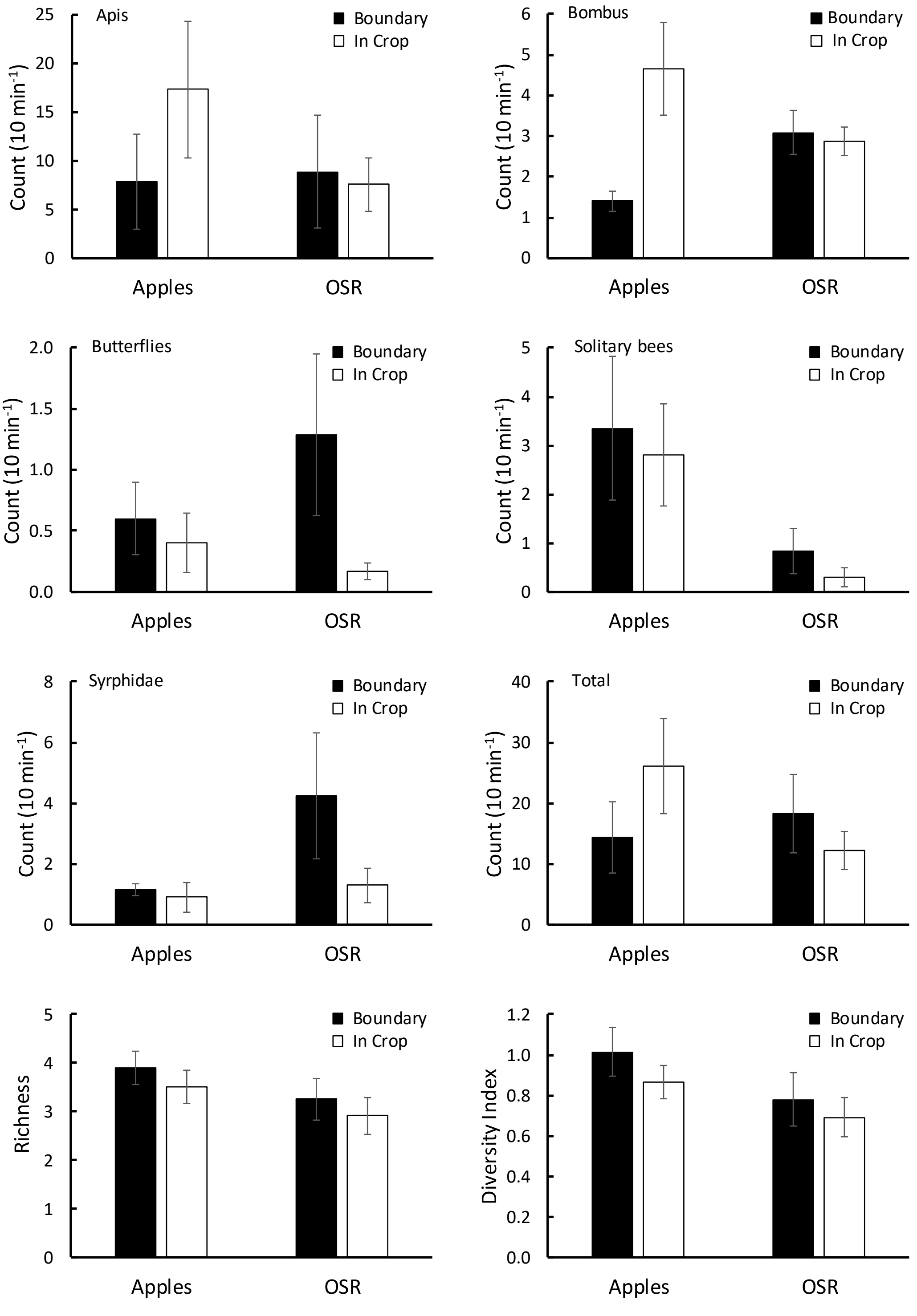


Figure 5. Abundance and diversity (mean ± SE) of pollinating insects in the centre of the main crop and in the field margins during flowering of OSR (n = 6) and apples (n = 5).

Table 3. Results of REML analysis (P-values) examining the response of insect abundance and pollinator diversity to: (A) crop type (APP v OSR) and location (crop centre v field margin) during the main crop flowering period (B) location (crop centre v field margin) and study period considering only the insects recorded in the apple sites and (C) crop type (APP v OSR) and study period considering the insects in both crops but only in the field margins. Insect abundance data were square root transformed before analysis. n.d.f. – numerator degrees of freedom.

(A)

	Crop type	Location	Interaction
n.d.f.	1	1	1
Apis mellifera	0.609	0.098	0.217
Bombus	0.588	**0.029**	**0.014**
Butterflies	0.756	**0.032**	0.158
Solitary bees	0.055	0.390	0.470
Syrphids	0.380	**0.027**	0.731
Total	0.709	0.462	**0.033**
Richness	0.348	0.063	0.859
Diversity	0.156	0.203	0.733

(B)

	Period	Location	Interaction
n.d.f.	2	1	2
Apis mellifera	**0.041**	0.639	**0.003**
Bombus	0.548	0.206	**0.017**
Butterflies	**0.003**	**0.012**	0.102
Solitary bees	**0.015**	0.213	0.409
Syrphids	**0.047**	**< 0.001**	0.316
Total	0.201	0.326	0.002
Richness	0.149	**< 0.001**	0.206
Diversity	**0.024**	**< 0.001**	0.247

(C)

	Crop type	Period	Interaction
n.d.f.	1	2	2
Apis mellifera	0.766	0.082	0.512
Bombus	0.106	0.430	0.466
Butterflies	0.245	< **0.001**	0.591
Solitary bees	0.445	**0.016**	0.124
Syrphids	0.118	**0.004**	0.524
Total	0.180	0.181	0.936
Richness	0.577	0.160	0.718
Diversity	0.669	0.092	0.845

3.4.2 Insects in the centre and field margins of apple orchards during and after main crop flowering

In the 120 ten-minutes surveys (total 20 hours of observations) performed in the apple orchards, a total of 1,488 pollinating insects were recorded, consisting of 595 *Apis mellifera*, 302 *Bombus* spp., 134 solitary bees, 394 syrphids and 63 butterflies. Eleven species of butterflies and six species of bumble bees were observed during the surveys, the most abundant being *Pieris* spp. and B. *terrestris*/*lucorum* agg. respectively (Appendix X).

Overall, there was steady decline in insect numbers over the three observation periods, with 810 insects observed in Period 1 (during apple flowering), 437 in Period 2 and 241 in Period 3 (Tab. 3B; Fig. 6).

Apis mellifera, *Bombus* spp. and solitary bees were most abundant during the main crop flowering period. Additionally, *Apis mellifera* and *Bombus* spp. were most abundant in the centre of the crop during this first period (Tab. 3B; Fig. 6). *Bombus* were evenly distributed between the centre and field margins in Periods 2 & 3, whereas *Apis mellifera*, although very much reduced in numbers, were more common in the field margins than the centre of the orchard.

Solitary bees showed no overall differences in abundance between the field centre and margins, and were very uncommon later in the season (Tab. 3B; Fig. 6). Butterflies and syrphids were both most abundant in the field margins compared with the centre of the crop, but whereas butterflies showed a dip in abundance in Period 2, there was a peak in hover fly observations in the same period (Tab. 3B; Appendix X; Fig. 6; see also Fig. 7).

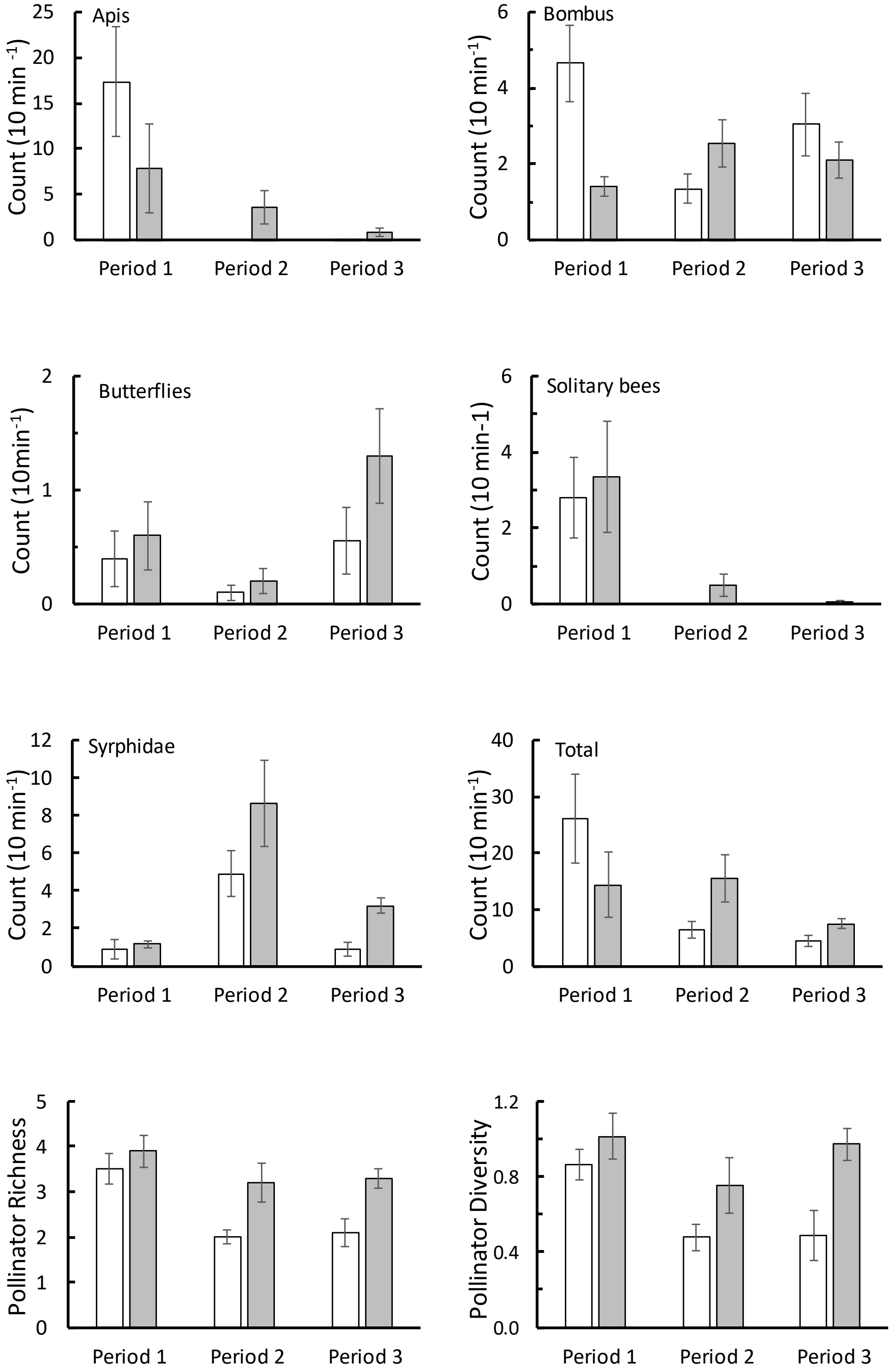


Figure 6. Abundance (mean ± SE) and diversity of pollinating insects in the centre of the crop (white columns) and field margins (grey columns) of apple orchards (*n* = 5) during (Period 1), 1-month after (Period 2) and 3-months after flowering (Period 3) of the main crop.

3.4.3 Insects in the field margins of both crops during and after the main crop flowering period

In the 132 ten-minute surveys (total 22 hours of observations) carried out during the three study periods in the field margins, a total of 2,015 pollinating insects were recorded, consisting of 522 *Apis mellifera*, 367 *Bombus* spp., 136 solitary bees, 848 syrphids and 142 butterflies. Sixteen species of butterfly, which represents just under half of the 33 species currently listed as resident in Ireland, and six species of *Bombus* recorded along the field margins over the three periods, with *Bombus terrestris*/*lucorum* agg. making up around 60% of the *Bombus* records (Appendix X).

No significant differences occurred between the apple and OSR crops in terms of abundance of any insect group and the diversity measures, and there were no significant statistical interactions between crop type and survey period (Tab. 3C; Fig. 7).

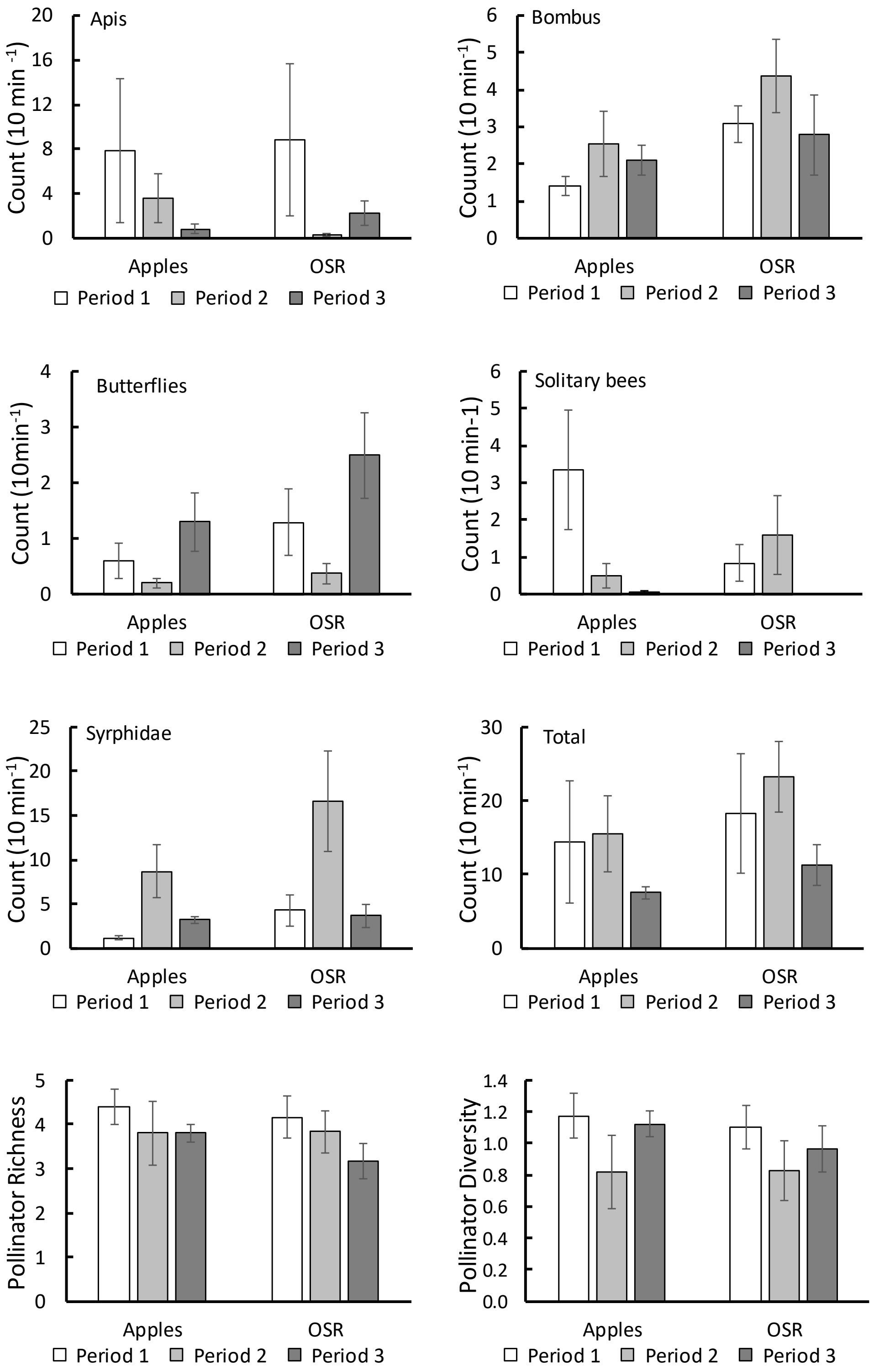


Figure 7. Abundance (mean ± SE) of pollinating insects in field margins during the flowering period (Period 1), 1-month after flowering (Period 2) and 3-months after flowering (Period 3) in OSR (n = 6) and apples (n = 5).

3.4.4 Flowering plants in the field margins during and after the main crop flowering period

Across the 33 site visits, 82 species of plants were observed in flower in the field margins; 73 species on the ground and 25 species in the ‘vertical’ hedge quadrats. Many plant species were relatively uncommon over the whole study period, and 41 of the 82 species recorded were only observed in one of the 33 surveys. Common species (> 30% of site visits) included *Rubus fruticosa*, *Ranunculus repens*, *Crataegus monogyna* and *Vicia sepium* (Appendix XI). The two most common flowering woody species flower in sequence (*C. monogyna* in May-June, and *R. fruticosus* June-August), whereas the two most common herbaceous species (*Ranunculus repens* and *Vicia sepium*) were in flower in all sampling periods.

There were no statistically significant differences between the apple and the OSR sites in terms of the field margin floral abundance and diversity measures (Tab. 4; Fig. 8), although abundance and diversity of field margin flowers did differ significantly among the three periods, the patterns being slightly different in the two crops, but in general these values were lowest in Period 3 (Tab. 4; Fig. 8).

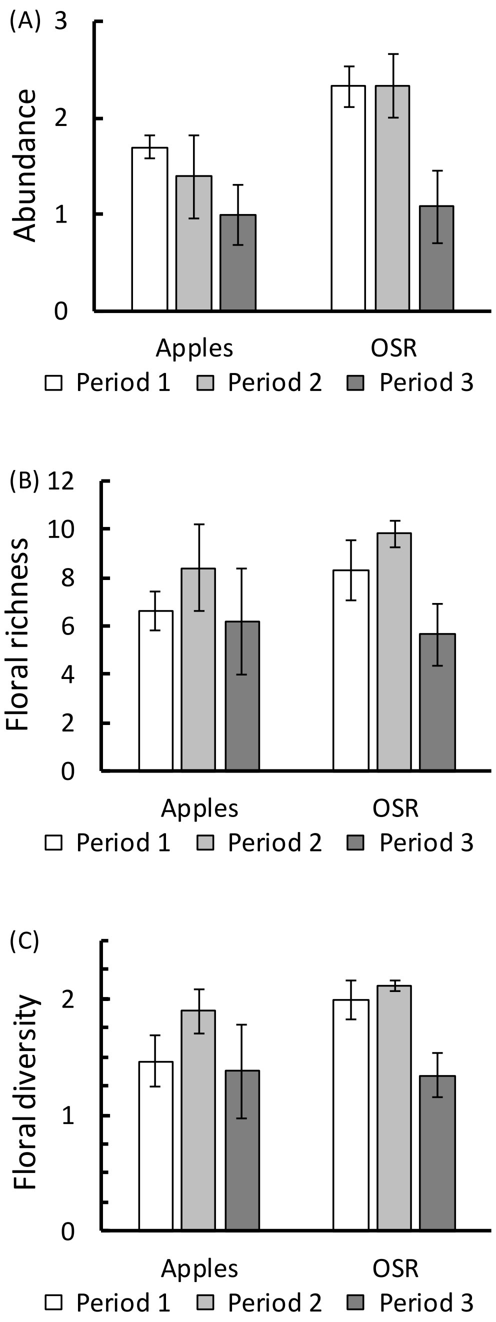


Figure 8. Abundance and diversity (mean ± SE) of entomophilous flowering plants in field boundaries during the flowering period (Period 1), 1-month after flowering (Period 2) and 3-months after flowering (Period 3) in OSR (n = 6) and apples (n = 5), where (*a*) median abundance score, (*b*) total species of species in flower, and (*c*) species diversity of flowering species

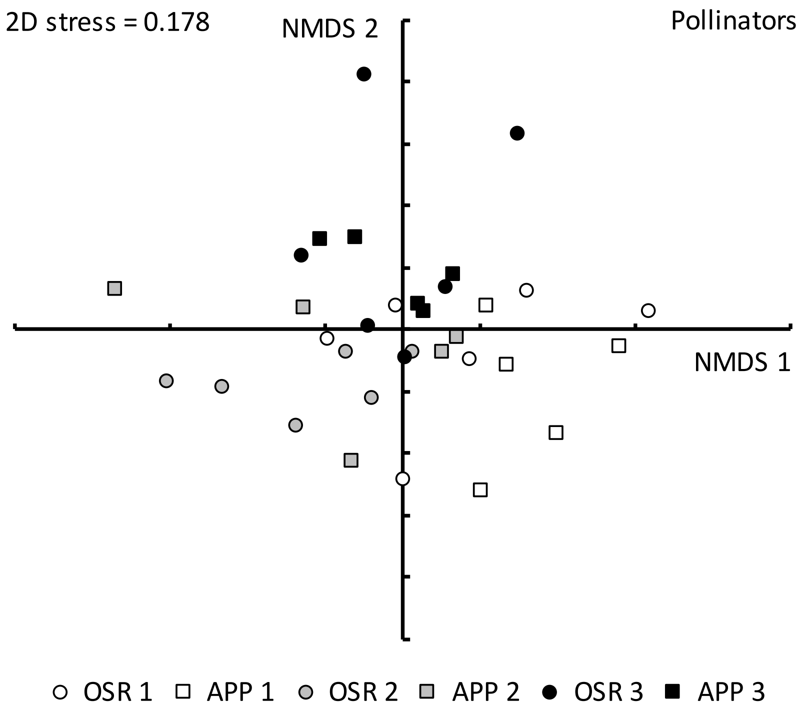
Table 4. Results of REML repeated measures analysis (*P*-values) examining the effects of crop type (apples/ OSR) and period (flowering period/ 1-month after flowering period / 3-month after flowering period) on abundance and diversity of flowering plants in the field boundary. Site was included in the REML model as a random factor. n.d.f. – numerator degrees of freedom; d.d.f – denominator degrees of freedom

	Crop type	Period	Interaction
n.d.f.	1	2	2
d.d.f.	9	18	18
Median abundance	0.137	**0.002**	0.272
Total species richness	0.610	**0.004**	0.373
Diversity	0.414	< **0.001**	0.068

3.4.5 NMDS analysis of insects and flowering plants in the field margin

For the assemblages of pollinating insects, the NMDS analysis did not distinguish the samples from the different crops in any study period (ANOSIM, P > 0.20) but did separate the assemblages recorded in the three different sampling periods into more-or-less distinct clusters (ANOSIM $P < 0.002$; Fig. 9). The Period 1 data were separated from that obtained in Periods 2 and 3 along NMDS Axis 1, whereas the Period 3 samples were separated from the Period 1 and 2 samples along NMDS Axis 2 (Fig. 9). Relative to Period 1, the Period 2 samples were associated with a high abundance of syrphids, whereas Period 3 was associated with low numbers of solitary bees and high numbers of butterflies (see also Fig. 7).

The ANOSIM procedure indicated significant differences among the floral assemblages obtained in the different periods ($P < 0.005$) and, accordingly, the NMDS analysis indicated that the field margin flora observed in Period 1 was separated from those obtained in Periods 2 and 3 along NMDS Axis 1, and that Periods 2 and 3 were separated along Axis 2 (Fig. 9). The only groups of samples not identified as significantly different were the OSR and apples clusters in Period 2 (P = 0.139), and the apple and OSR clusters in Period 3 ($P = 0.115$). From the NMDS plot, this result is visualized as a separation of the floral assemblages in OSR and apple crops in Period 1, but a convergence of the field margin floras in the two crops in the latter periods (Fig. 9). The Period 1 samples were associated with relatively high abundances of *Crataegus monogyna* and *Taraxacum officinale* (L.) Weber ex F.H. Wigg whereas the Period 2 and 3 surveys performed later in the year were associated with *Rubus fruticosus* and *Geranium robertianum* L. (Appendix XI).



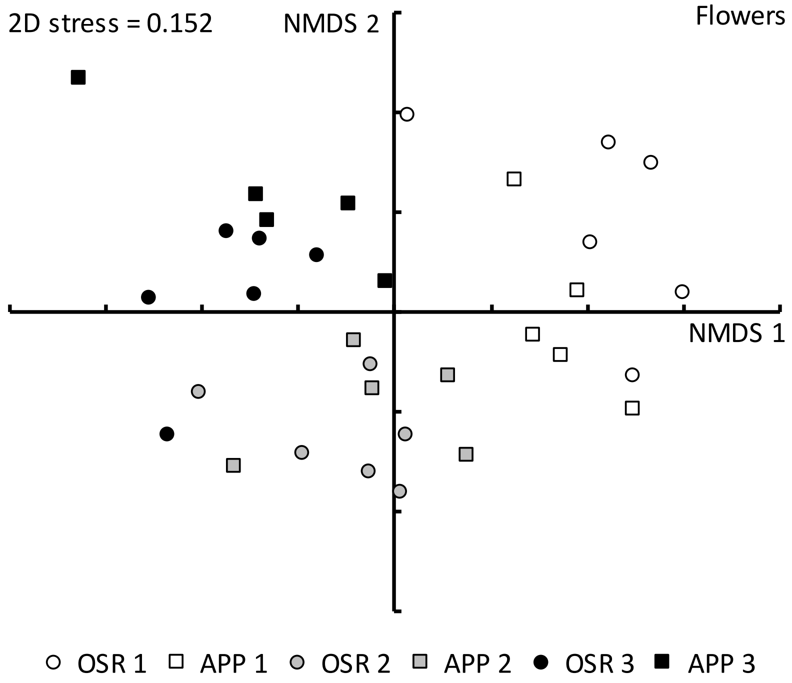


Figure 9. NMDS plots based on abundance of five groups of pollinating insects occurring in field margins and relative frequency of field boundary flowering plants in apple orchards (APP) and OSR during the main crop flowering (Period), 1-month after flowering (Period 2) and 3-months after flowering (Period 3).

3.4.6 Relationships between insects and floral assemblages

Only weak to moderate correlations (rS < |0.4|) were found between the abundance and diversity of insects and flowering plants (Fig. 10; Tab. 5). The abundance of *Apis mellifera* and solitary bees showed no significant correlations with any plant measure, whereas the abundance of *Bombus* spp. ($P< 0.05$) and syrphids ($P< 0.1$) were moderately correlated with floral diversity (H). The abundance of butterflies was negatively correlated with floral species richness (S) (Fig. 10; Tab. 5). The number of insect groups present (S) and insect diversity (H) were not correlated with any measure of flower abundance or diversity (Tab. 5).

A Mantel test based on rank correlations of the similarity matrices used for the NMDS indicated a weak, although statistically significant, positive relationship between the patterns seen in the insect and floral assemblages seen in the field margins of the different crops over time (rS = 0.133, $P< 0.025$).

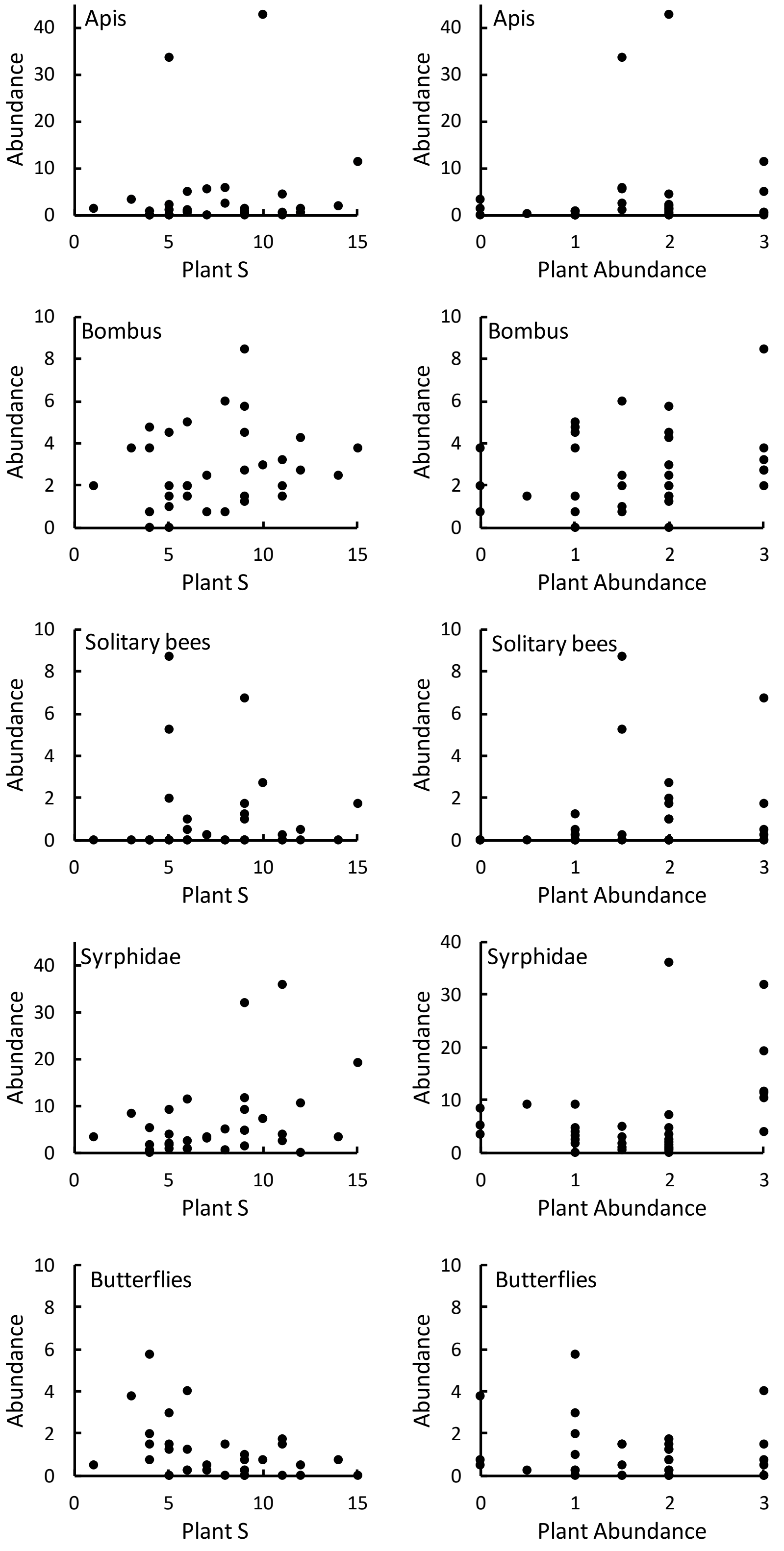


Figure 10. Scatterplots illustrating relationships between abundance of pollinating insects (mean counts per 10 min) with species richness and abundance (median abundance score) of field boundary flowering plants over three study periods.

Table 5. Spearman's rank correlation coefficients (r_S) showing strength and direction of relationships between attributes of pollinating insect assemblage and diversity and abundance of flowering plants in field boundaries during 3 site visits. [Critical values of r_S with n = 33, P< 0.05 |0.356|** and P< 0.1 |0.301|*].

		Floral variables		
		Median abundance	Flower diversity *H*	Flower richness *S*
Insect variables	*Apis mellifera* abundance	0.153	0.151	0.176
	Bombus abundance	0.197	0.356**	0.228
	Solitary bee abundance	0.292	0.184	0.197
	Syrphid abundance	0.196	0.337*	0.328*
	Butterfly abundance	- 0.134	- 0.327*	-0.394**
	Total abundance	0.290	0.365**	0.301*
	Insect *S*	0.167	0.248	0.179
	Insect *H*	0.057	- 0.002	- 0.027

3.5 Discussion

In the context of our study set in the grass-based Irish agricultural landscape, these results demonstrate that pollinating insects are relatively abundant in field margins even when these margins enclose an in-flower mass-flowering crop, but also highlight that this pattern is highly taxon specific. In particular, honey and bumble bees were more abundant in the crop during its flowering period, but hover flies and butterflies were more prevalent in the boundaries. This could be because social bees can fly relatively long distances to visit mass-flowering resources (Osborne et al. 2007), and because of the other resources offered by boundaries for other insects (e.g. mating and oviposition sites, and larval microhabitats) (Power & Stout 2011). The assemblage of field margin pollinating insects shifted in time relative to the crop flowering period, a pattern also shown by the assemblage of field margin flowering plants, although there were no general relationships between insect abundance and diversity with the quantity and diversity of flowers available.

In an Irish landscape dominated by improved grassland, field margins and hedgerows might be expected to provide refuge, food and larval resources for various groups of pollinating insects (Power & Stout 2011; Volpato et al. 2020). Indeed, Stanley & Stout (2013) reported that all pollinating insect groups were more abundant in field margins compared to the crop centre for a range of crops. However, when mass-flowering crops such as OSR are in bloom, this pattern can change. For example, Walther-Hellwig & Frankl (2000) found there were more *Bombus* in OSR than in the hedgerows or field boundaries. During the main crop flowering period, we found no evidence that any insect group was more abundant in the centre of the OSR crop compared with the field margins, but that, in turn, only some groups, such as butterflies and syrphids, showed a distinct preference for field margins. During the flowering period for both apples and OSR, adult butterflies and syrphids are not entirely driven by requirements for pollen and nectar, and the wild plant species present in the field margins offer resources for both adults and their offspring, for example host plants for lepidopteran larvae and prey and for aphidiphagous syrphids (Potts et al. 2009; Stanley & Stout 2013). The occurrence of honey bees and solitary bees in both the centre and margins of the OSR crop suggest these different habitats offer alternative and/ or complementary resources, and it is known that many wild flowers share pollinating insect species with OSR (Zurbuchen et al. 2010; Jauker et al. 2012; Stanley & Stout 2014; Coudrain et al. 2016).

Although it has been shown that *Bombus* colonies do not perform well in a landscape dominated by apple orchards (Proesmans et al. 2019), our results indicated that *Bombus* showed a preference to forage on apple blossoms compared with adjacent field margins during Period 1 (April-May). This pattern may have been accentuated by the presence of managed *B. terrestris* colonies on site, and thus larger number of individuals, during the apple flowering period, but was also observed in non-commercial species (20 individuals in the centre of the crops and 12 in the field margin). The syrphids and butterflies showed a general preference for the field margins over the main crop in all three study periods, and, because *A. mellifera* and solitary bees were recorded primarily in the field margins after flowering had ceased, insect diversity and richness were, as a consequence, highest in the field margins.

When assessing the field margin insect assemblages in both crops over the three periods, we found taxon specific differences in abundance among study periods but no significant differences between the two crops. *Apis mellifera* did not show any temporal shift, at least in the field margins, which was unexpected as some beekeepers moved colonies to new sites once flowering ceased. The abundances of solitary bees, hover flies and butterflies all differed among the three study periods, but all three groups exhibited different patterns. These phenological shifts in abundance and/-or activity of adult hover flies and butterflies have been reported previously (Ball & Morris, 2015; Bond & Gittings 2008; Cole et al. 2017): many species of butterfly in Ireland are known to exhibit such seasonal ‘bimodal’ peaks in abundance, resulting from an early population of adults breaking hibernation, followed by a later generation arising from their offspring (Bond & Gittings 2008).

The changes in relative abundance of the five insect groups among study periods resulted in a temporal shift in the composition of the field margin insect assemblage. There were no differences in the composition of the field margin insect assemblages found on the two crops, possibly because, even when a mass-flowering event occurs, field margins represent a consistent feature occurring through the relatively homogeneous Irish agricultural landscape, and because we only identified insects to functional groups. Seasonal shifts in insect abundance have been reported in several previous studies, and their interactions with naturally-occurring flowering plants will likely change once the numerically-dominant (crop) flowers are no longer present (e.g. Stanley & Stout 2014; Tiedeken & Stout 2015; Kovács-Hostyánszki et al. 2019).

The abundance of floral units and diversity of entomophilous flowers in the field margins also varied significantly among study periods, although, as with the insects, there were no differences between the OSR and apple sites. In terms of composition of the floral assemblage, a similar temporal shift was observed as was seen for the insects, although some separation of the floral assemblages occurred between OSR and apples in Period 1, probably because OSR flowered earlier and so sampling Period 1 occurred several weeks earlier than in apples (Appendix IV). The results of the Mantel test also indicated that these temporal shifts in the assemblages of entomophilous flowers were associated with parallel temporal shifts in the composition of the insect assemblages, suggesting that the composition and structure of insect-plant interaction networks within each site would also shift with time (Rotenberry 1990; Timberlake et al. 2019).

There are many examples of positive relationships occurring between field margin plant diversity/abundance with the diversity/abundance of pollinating insects, for example: honey bees (Sanchez et al. 2019), wild bees (Power and Stout 2011; Kovács-Hostyánszki et al. 2019), *Bombus* (Potts et al. 2009; Purvis et al. 2020), butterflies (Potts et al. 2009; Wix et al. 2019) and syrphids

(Sutherland et al. 2001; Cole et al. 2017). In our study, the different pollinator groups exhibited different temporal patterns in abundance, so we felt it was unlikely that we would see any consistent relationships between insect abundance and the abundance and diversity of floral resources in the field margins: fittingly, the correlations we observed were generally weak. This finding may represent a true situation when pollinator metrics are correlated with floral components over time, although the lack of statistically-significant relationships may have also reflected numerous methodological aspects of our study: the coarse measures of abundance we used for floral units, the pooling of insects into higher taxonomic groups, some spurious high counts of insects, and the prevalence of zero counts for some taxa in some periods. We did identify positive correlations between floral diversity and *Bombus* abundance and the total abundance of pollinating insects, which is in general agreement with the studies given above. The lack of relationship between the numbers of syrphids and floral abundance and diversity is similar to that reported by Power & Stout (2011), and so is at least consistent in the context of Irish field margin insects set in pasture-based agriculture.

We acknowledge that our results were obtained from only a single growing season, and that the sample size, in terms of study sites, offered low statistical power for the detection of weak effects. Additionally, spatial or temporal patterns that may occur for individual species may have been lost by pooling our insect records into higher taxonomic groups, and we have not considered variation in field boundary type within and between study sites. If practicable, future studies would likely benefit from achieving species-level identifications to gain more detailed insight into the autecology of individual pollinator species, and also by examining the robustness of any habitat or temporal responses by assessing their repeatability over multiple growing seasons.

Nonetheless, the data we obtained enabled us to address the original aims of the study, and confirm that hedgerows and field margins, even when they border a flowering crop, represent an important habitat for major pollinating insect groups. Our findings therefore add additional impetus to the adoption of agri-environment schemes where the protection and improvement of field margins is used as a means of retaining and/ or enhancing farmland biodiversity. Although the composition of the field margin pollinating insect assemblage shifted in time, parallel to changes in the floral assemblage, in our system, insect abundance and diversity were not strongly related to floral abundance and diversity, at least at the physical scale of our study and using our abundance and diversity metrics. Thus, any assessment or scoring of sites based on field margin biodiversity should consider seasonal changes in insect and plant abundance and be conscious that indicators or indices of farmland biodiversity or conservation success based on pollinating insects may not always be correlated with similar indices based on flowering plants.

3.6 Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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CHAPTER 4

Habitat diversity and larval diet influence solitary bee fitness in European landscapes

To be submitted to Journal of Applied Ecology as: “Habitat diversity and larval diet influence solitary bee fitness in European landscapes” – Irene Bottero, Matthias Albrecht, Anina Knauer, Simon Hodge, Robert Dean, Steffen Hagenbucher, Christophe Dominik, Olivier Schweiger, Simon Potts, Marika Mand, Alexandra-Maria Klein, Giovanni Tamburini, Helena Pereira-Peixoto, Cecilia Costa, Gennaro di Prisco, Piotr Medrzycki, Pilar de la Rúa, Vincente Martínez López, Daniel Dzul Uuh, Joachim de Miranda, Maj Ründolf, Estefania Tobajas Talavan, Janine Schwarz, Mark Brown, Jane C. Stout

4.1 Abstract

Osmia bicornis (synonym *O. rufa*, red mason bees) are cavity-nesting bees that supply their nests with pollen, to provide the nutrition necessary for larval development. *O. bicornis* are commonly present in European agricultural landscapes, where they are managed to pollinate entomophilous crops, including apples and oilseed rape. Although polylectic, females may focus on locally abundant pollen sources, including mass-flowering crops, trees and herbaceous plants. The nutritional composition of pollen can impact on *O. bicornis* fitness and lack of appropriate floral resources in intensively managed agricultural habitats can constitute a threat for this species. Our study investigated the relationship between the type of pollen collected (botanical origin and diversity), the composition of the landscape (habitat type and diversity) and the fitness of *O. bicornis*. A total of 288 *O. bicornis*-primed trap nests were deployed, each containing approximately 100 separate nesting tubes. Three nests were located in each of eight oilseed rape fields and eight apple orchards, in six countries across Europe. We recorded the local flowering diversity, classified the surrounding habitat types in a 1km radius and analysed the pollen provisions in the nests, during the peak crop flowering period. We related these variables with measures of *O. bicornis* fitness, including the rate of hatched pupae and dead larvae, the number of the adults produced the following year and their sex ratio and weight. We found that a higher percentage of non-crop pollen in nests was positively correlated with the number of adults produced the following year. However, adult female weight was negatively correlated with the proportion of pollen from non-crop plants. There was a higher rate of occupation of the cells in the tubes from nests in oilseed rape fields rather than apple orchards, suggesting that crop type and probably its management, plays a role in the fitness of these bees. There was a higher percentage of non-crop pollen in nests located in sites with more non-cultivated habitat in the surrounding area and with greater habitat diversity, but more crop pollen in nests from oilseed rape sites. Overall, our results support the importance of preserving non-crop pollen sources in agricultural landscapes, particularly in those containing mass-flowering crops.

Keywords: *Osmia rufa*, non-crop pollen, habitat composition impact

4.2 Introduction

Much of the understanding of bee decline derives from studies conducted on honey bees and bumble bees, while information focusing on wild bees is limited (Saunders et al., 2020). Hence, this study focused on *Osmia bicornis* (synonym *O. rufa*) and investigated how landscape configuration and pollen type (botanical origin and pollen diversity) impact its fitness.

O. bicornis is a univoltine wild bee species, commonly known as red mason bee. This species is present across Europe and it is one of only a few solitary bee species that are managed as pollinators for entomophilous crops, including apples and oilseed rape (Jauker et al., 2012). *Osmia bicornis* nests in above-ground cavities, including plant stems and holes in cliffs and masonry. Within a cavity, the female bee constructs a series of cells, each of which is provisioned with pollen, on which an egg is laid and the cell subsequently sealed (Splitt et al., 2021). The position of the cell in the cavity is related to the sex of the individual, where females eggs are usually laid first, deeper in the cavity and males are towards the entrance. This should reduce the risk of predation for the females and result in an earlier hatch of the adult males the following spring (this species is protoandrous; Raw 1972; Holm 1973; Seidelmann 1995).

The main food resource for the developing individuals inside the cells is pollen, mixed with a little nectar. Pollen is collected from surrounding habitats by the females (Westrich et al., 1989). Although polylectic, it has been reported that *O. bicornis* will focus on abundant pollen and nectar resources, such as mass-flowering crops, trees and weedy herbs, to maximise efficiency (Persson et al., 2018; Splitt et al., 2021). Preferences emerge for those floral species that provide higher quality pollen (Bukovinszky et al., 2017). Pollen from non-crop plants (such as *Quercus* spp., *Ranunculus* spp., *Acer* spp., *Juglans* spp., *Papaver* spp.) have been shown to be preferred over other cultivated groups (e.g. *Brassica napus*; Ruddle et al., 2018; Teper, 2007) and the presence of natural features around the nests (at a 1 km radius) has been correlated with more cocoons (Bednarska et al., 2022). However, mass-flowering crops have been associated with high food provision, providing a source of pollen during their flowering period. Oilseed rape crops, for example, provide valuable nectar for adults, enhancing their population sizes (Jauker et al., 2012; Holzschuh et al., 2013). In addition, an increase in the cocoon mass was found with larger areas of oilseed rape crops in the landscape (Bednarska et al., 2022). Nevertheless, pollen from crops has been associated with high pesticide residues, with an increased exposure risk for bees (Centrella et al., 2019; Zioga et al. 2020).

Diverse diets might affect *O. bicornis* fitness. On one hand, pollen composition impacts on the larval growth and performances, due to changes in nutritional composition or to the presence of toxic compounds (Levin and Haydak, 1957; Stanley and Linskens, 1974; Roulston and Cane, 2000). On the other hand, the quantity of pollen consumed by the larvae affects *O. bicornis* adult weight (Wilkaniec et al., 2004; Radmacher and Strohm, 2009), impacting on their fitness. The weight of adults is related to fitness for both females and males. Heavier females perform better in their foraging flights (Abrol and Kapil, 1994; Giejdasz, 1998) and in usurping conspecific nests (Kim, 1997; Tepedino and Torchio, 1994). Heavier males are more competitive during mating and for the territorial defence (Alcock, 1995; Alcock, 1997; Berg et al., 1997; Severinghaus et al., 1981). For these reasons, the availability and distribution of floral resources in the landscape modulates foraging behaviour of *O. bicornis.* The lack of floral resources in the proximity of suitable nesting sites forces females to fly further to find pollen (Müller et al., 2006, Roulston and Goodell, 2011). The length of provisioning flights has repercussions for offspring survival, due to different energy costs and because longer foraging flights are associated with higher risk of nest predation (Müller et al., 2006; Seidelmann, 2006; Roulston and Goodell, 2011). Likewise, females regulate their sex investment to maximise reproductive success according to the resources available, with a shift of sex ratio towards females and an increase of offspring size as a consequence of increasing pollen provisions (Rosenmhein et al. 1996; Kim, 1999). Hence, both the quantity and quality of pollen collected by adult foragers affects the chances of larvae successfully growing, pupating and surviving to form the next generation, as well as the size of individuals and sex ratio of that next generation.

There is mixed evidence, however, concerning both the role of pollen (cultivated and non-cultivated plant species) on *O. bicornis* development and fitness and the risk associated with intensively managed crops (application of plant protection products and the depletion of semi-natural habitats associated with diverse diets and potential nesting sites; Goulson et al., 2005; Teper, 2007; Potts et al., 2010 a; Jauker et al., 2012; Holzschuh et al., 2013; Bukovinszky et al., 2017; Persson et al., 2018; Ruddle et al., 2018; Centrella et al., 2019; Splitt et al., 2021; Bednarska et al., 2022). This indicates the need for investigating the relationship between pollen types (pollen diversity and pollen of non-crop origin) and landscape context (extent and diversity of habitats surrounding crop fields) on the development and fitness of *O. bicornis* nesting in mass-flowering crop fields. Our study aims to add new insights in such a context. Using a standardised approach, we studied the relationship between habitat and pollen diversity and origin (crop and non-crop) with different developmental stages of *O. bicornis,* across 96 sites in six European countries.

We predicted that *O. bicornis* developmental stages would be positively correlated with the percentage of pollen belonging to non-crop species of plants, despite the availability of pollen from cultivated crops (in bloom when the study was conducted). We also tested whether the landscape surrounding target crops at a 1 km radius around the sites (percentage of non-cultivated habitats and habitat diversity), affected the pollen stored in cells and the occupancy of nests by *O. bicornis*. We hypothesised that the diversity of pollen stored in the cells and a percentage of pollen of non-crop origin, could be positively related with *Osmia bicornis* fitness and development. In addition, we hypothesised that the percentage of non-crop pollen present in the pollen stock would depend on the surrounding landscape composition, increasing with the percentage of non-cultivated and diverse habitat surrounding sites. Ultimately, we hypothesised that non-cultivated habitats would be related to a higher occupancy of the nest.

We found that more adults hatched in those sites where we found more pollen (percentage) belonging to non-crop plants. In addition, we found more pollen of non-crop plants in those sites that were surrounded by higher percentages of non-cultivated habitats and more diverse habitats. This suggests that non-crop habitats might positively impact on *O. bicornis* fitness, providing them with abundant high quality pollen. Our results open new insight on the importance of pollen of non-crop origin for *O. bicornis* in a wide geographical context, contributing to better understanding of the requirements of this species to proliferate in the European agricultural landscape.

4.3 Methods

4.3.1 Site selection

This study was conducted in six countries – Estonia, Germany, Italy, Spain, Sweden and Switzerland – as part of the PoshBee project network (https://poshbee.eu/; Fig. 11). In each country, sixteen sites were selected, representing typical annual and perennial European entomophilous crops, namely eight winter-sown oilseed rape fields (OSR; *Brassica napus*) and eight apple orchards (APP; *Malus* spp.), giving a total of 96 sites. (Fig. 11). Sites were at least 5 km distant, to increase the chances of ecological independence between sites, with the exceptions of two sites located in Spain, that were 3 km apart (see Hodge et al., 2022).

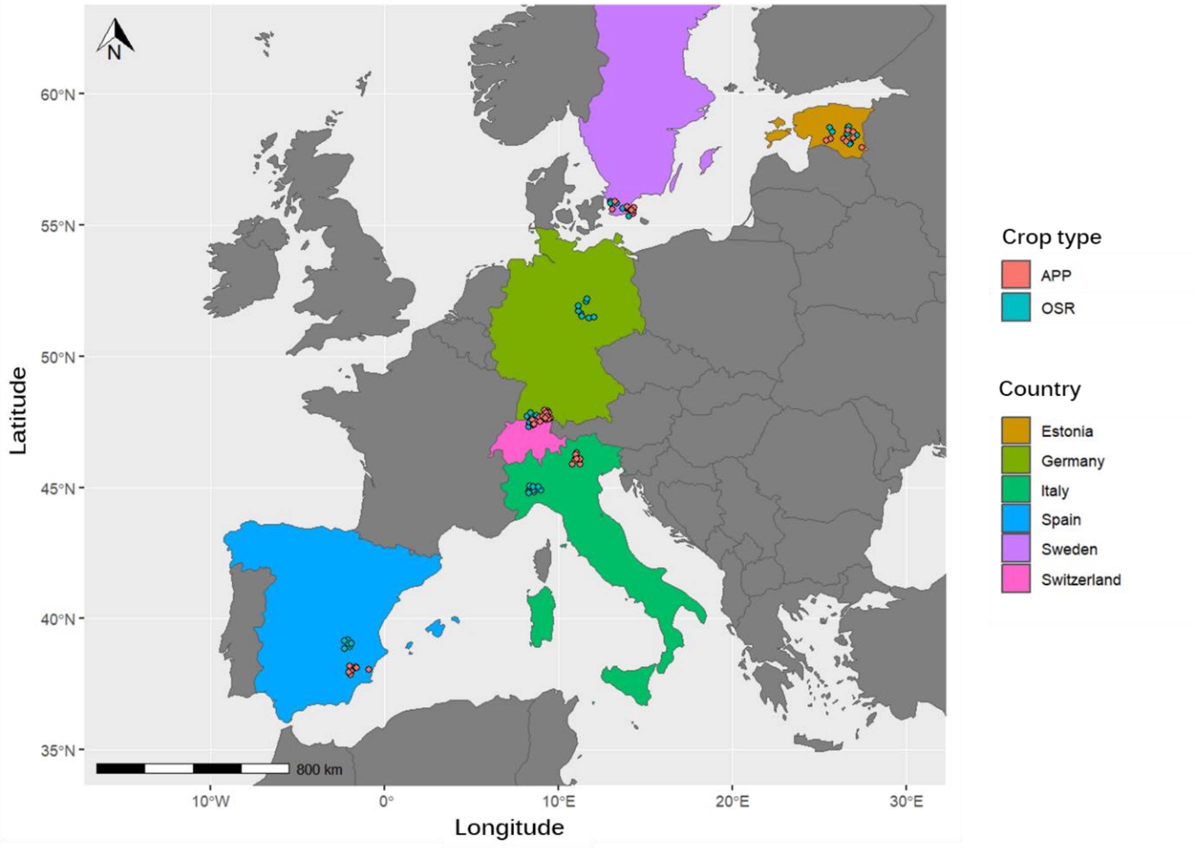

Figure 11. Map of the sites across Europe. The coloured states are the countries that participated in the study (Spain, Italy, Switzerland, Germany, Sweden, Estonia). The blue dots represent the location of the oilseed rape sites, while the red ones the apple orchards. Longitude and Latitude are represented on the axes (x and y).

4.3.2 Deployment and monitoring of trap nests

Between three and seven days before the flowering period of the target crops (spring 2019), three *Osmia bicornis* trap nests were set on the one of the border of the fields, in each site (Hodge et al. 2022; Appendices XII and XIII). Nests (supplied by Red Beehive, UK) comprised a 15 cm length plastic pipe, sealed at one end, and filled with approximately 100 cardboard tubes of 7.5 mm diameter. Each nest was initially primed with approximately 100 *O. bicornis* pupae (provided by Wildbiene & Partner), with a sex ratio of 1:1 (female:male), in an emergence tube. Prior to establishing in the field sites, pupae were stored at 4°C, but were brought to 10°C degrees before being placed in the field, to induce the end of the diapause (Appedix XIII). The nests were placed along a south-facing field boundary, on a pole/support at 1-1.5 m from ground level (Hodge et al., 2022). Nests had their entrances tipped a few degrees (<10°) down from horizontal to reduce the risk of water accumulation during heavy rain, and after 10 days in the field, the emergence tube was removed and replaced with spare cardboard tubes so that any pests/parasitoids in the founding stock did not emerge and immediately contaminate the new nest tubes, developing larvae and pupae .

At the end of the flowering period (Appendix XII) a 0.5 x 0.5 mm was placed on all the nests, to exclude the entrance of further bees and enemies. Nests were left in the sites until late September-mid October 2019, to allow the development of the larvae. In October 2019, the mesh was removed and some cardboard tubes from each site were collected and labelled. Despite an original intention to collect 30 tubes from each site (10 from each nest), each country had to adapt this number due to the different condition of their sites and nests (Appendix XIII). This led to a varied number of collected tubes. Tubes were opened in the lab, and the number of chambers built in each one of these tubes was recorded, and for each one those we counted the number of cells containing pupae, dead larvae or just pollen. For each nest, cells containing only pollen and dead larvae were divided by the total number of cells to calculate the rate of mortality, while the cells containing pupae were divided by the total number of cells to estimate the rate of survived pupae. The number of chambers built in each nest and the number of tubes occupied per nest were used to estimate the occupation of the nests.

The remaining tubes were removed from the fields, labelled, and stored in glass tubes at controlled condition (2°C; 60%-80% humidity), to simulate the hibernation until the late March of the following year (spring 2020). The end of the hibernation period was simulated, bringing the tubes to a temperature of 10°C for one week (60%-80% of humidity). *O. bicornis* individuals emerged from those tubes were recorded, as well as their sex and weight. Any emerging enemies (parasitoids flies, wasps, beetles and mites) were also recorded (Appendix XIII).

4.3.3 Pollen collection and palynological analyses

During the peak of the flowering season approximately ten cardboard tubes were collected from each site, and replaced by new, empty cardboard tubes (Appendix XIII). The tubes were marked and stored in plastic bags in the freezer (at – 20°C), and subsequently opened and an equal proportion of pollen from all the nest tubes was extracted (minimum required quantity from each site 15.1 g) and stored at – 20°C, until posted to the Agricultural and Environment Research Centre (CREA) in Bologna, Italy, for palynological analyses (Hodge et al., 2022).

Out of each samples, 1.0 g of pollen was used to create a solution in 20 ml of distilled water, and its sediments were spread on a 18x18 mm surface on a microscope slide. One drop of glycerine was added to the slides, once dried, and successively the examined at 400X magnification. Two reads were performed to identify the pollen grains, for a total of 500 grains counted and identified, comparing them with those present in the collection of reference slides in CREA. Those grains that were non-identifiable or non-identified were excluded, while the damaged grains were counted, when their identification was possible. The final data were obtained calculating the percentage of each group of each group of pollen, out of the total counted grains per site.

For our analyses, we grouped for each site pollen belonging to cultivated crops and non-crop species. Some groups of plant contained both cultivated and wild species (for example *Brassica* and *Malus*), and so we attributed pollen origin depending on the cultivation present in the area of the sites. Thus even though *Brassica* spp. includes wild species, we categorised pollen as “crop” when the nests were located in oilseed rape crops (*B. napus*). Similarly, all Malus spp. pollen was considered as cultivated. *Citrus* spp., *Oleacea* spp. and *Vitis* spp. were also attributed to cultivation, while other plant groups were all included in the “non-crop” plants (Appendix XIV).

4.3.4 Habitat data

To investigate the land use around the sites, we mapped the landscape at a 1 km radius around the target crops, using the geographic information system (ArcGIS Pro 2.4.1, ESRI), based on high resolution images provided by World Imagery (ESRI). Land cover, mapped at a 1:2500 scale, was classified using the EUNIS habitat classification into different categories; although while the EUNIS system offers a detailed classification of each land-cover that best defines ecological habitats, we harmonized and reclassified the land cover categories in accordance with the habitat requirements of flower-visiting insects. Therefore, woodlands, shrubby areas, hedgerows, lines of trees and gardens were combined into the same land-use cover class (non-cultivated habitat), under the assumption that they positively benefit flower-visiting insects by providing potential nectar, pollen or nesting resources (Marshall &Moonen, 2002, Marini et al., 2012, Alison et al., 2021). We used this land cover type to estimate the impact of non-crop habitats on the pollen stores in the tubes chambers and on the occupancy of the nests by *O. bicornis* bees. To quantify the habitat diversity of the landscape surrounding the sites, we used the Shannon diversity index (SHDI) that was calculated using the different categories obtained from a 1 km radius around the target crops (Surface Running Waters, Waterbodies, Wetlands, Grasslands including both managed grassland for livestock, and semi-natural grassland, non-crop habitats, Bare Areas, Apple Orchards, Arable Crops including different cultures and different types of management, and Urban Areas including different type of sealed areas such as roads and cities).

4.3.5 Statistical analyses

We performed the analyses using the software Rstudio (Version 1.3.1093).
The occupation rate of the nests was calculated as the number of chambers divided by the number of collected tubes for each site. The number of cells only containing pollen and containing dead larvae, divided by the total number of chambers gave the initial rate of mortality. The number of cells with pupae divided by the total number of cells expressed the rate of hatched pupae.

The number of emerged adults the next spring (2020), could not be compared with the initial number of hatched pupae or colonised cells because those values were assessed by random collection of tubes in the nests and successively removed. For this reason, the number of emerged bees was used as measure *per se* for each site. The sex ratio of the individuals emerged in March 2020, was calculated as the number of males, over the total number of alive individuals for each site. The mean of the weights of the emerged individuals was used to calculate the average weight of females and males for each site.

Not all the countries could collect all the required data, and so for each life stage a different set of countries was analysed, specifically: the rate of nest occupation was collected in all six countries; the rate of hatched pupae and mortality were collected in Spain, Estonia, Germany (only

OSR sites), Italy and Sweden; adults hatched in spring 2020 and their sex ratio were recorded in Spain, Germany (only OSR sites), Italy and Sweden; the weight of hatched adults was recorded in Spain, Germany (only OSR sites) and Sweden (Appendix XV). Moreover, data about the abundance of different groups of parasitoids were collected in Germany (only OSR sites), Italy and Sweden.

To investigate the relationship between the landscape and the pollen collected in the nest and on nest occupation, we created mixed effects models where the number of occupied cells, pollen diversity, percentage of pollen from non-crop species were the response variables and the class areas of non-cultivated habitat, the habitat diversity, the crop type and the flower richness were the predictor variables. To investigate the impact of the landscape on the pollen types, the amount of pollen over the total collected (for each site) was investigated using binomial family in the models, while for the other models we used Gaussian family.

Similarly, mixed effects models were used to assess the relationship between pollen diversity, and percentage of non-crop pollen, and the different life stages of the bees. In all the models, country was considered as random effect. When necessary, we accounted for over-dispersion adding an observer term to the random effect. The function stepAIC() was used to select the best model (MASS package). A Poisson distribution was used in the models investigating the number of alive bees, while a Beta distribution was used in the investigation of sex ratios. The rate of hatched pupae and mortality were investigated using binomial family. Gaussian or Gamma distribution were used in the other models.

Model diagnostics were run for each model, to check if all statistical requirements were met.

Parallel analyses were run, inserting parasitoid abundance into the models as a covariate, for those countries that recorded these data. Since the results did not change, and the datasets containing parasitoids were not available for all the countries and contained missing values, we decided not to investigate this parameter further.

General Linear models (package “MASS”) were used to investigate the relationship between crops and country and pollen characteristics (the percentage of non-crop pollen and the percentage of different species of pollen in the record). A t-test was run to test differences between the weight of the pollen in the two crops, and between the number of grains collected from *Brassica* spp. or *Malus* spp..

4.4 Results

4.4.1 Pollen stock in the nests

Overall, 68 pollen types were identified (Appendix XIV) but there were no differences in the number of pollen types between the countries or the two crop types (t-value=0, *P*=1; Fig. 12). Across all the countries and in sites containing the two types of crops, some pollen types dominated, namely Acer spp., *Brassica* spp., *Juglans* spp., *Malus* spp., *Papaver* spp., *Quercus* spp., *Ranunculus* spp., Salix spp. were all found to comprise more than 10% of the pollen loads. Out of the pollen identified, five groups belonged to cultivated plants and the rest belonged to non-crop species (see Appendix XIV). Differences were found in the percentage of non-crop pollen in different countries and crops, with non-crop pollen less present in oilseed rape crops and in Germany, and more abundant pollen belonging to non-crop species present in Spain, Estonia and Italy (*P*<0.001; *z*-values respectively: -10.10, -12.319, 4.25, 3.35, 6.28; Fig. 13). Within cultivated pollen, *B. napus* pollen was more abundant compared to *Malus* spp. (t= -2.49, df = 143.75, *P*=0.01).

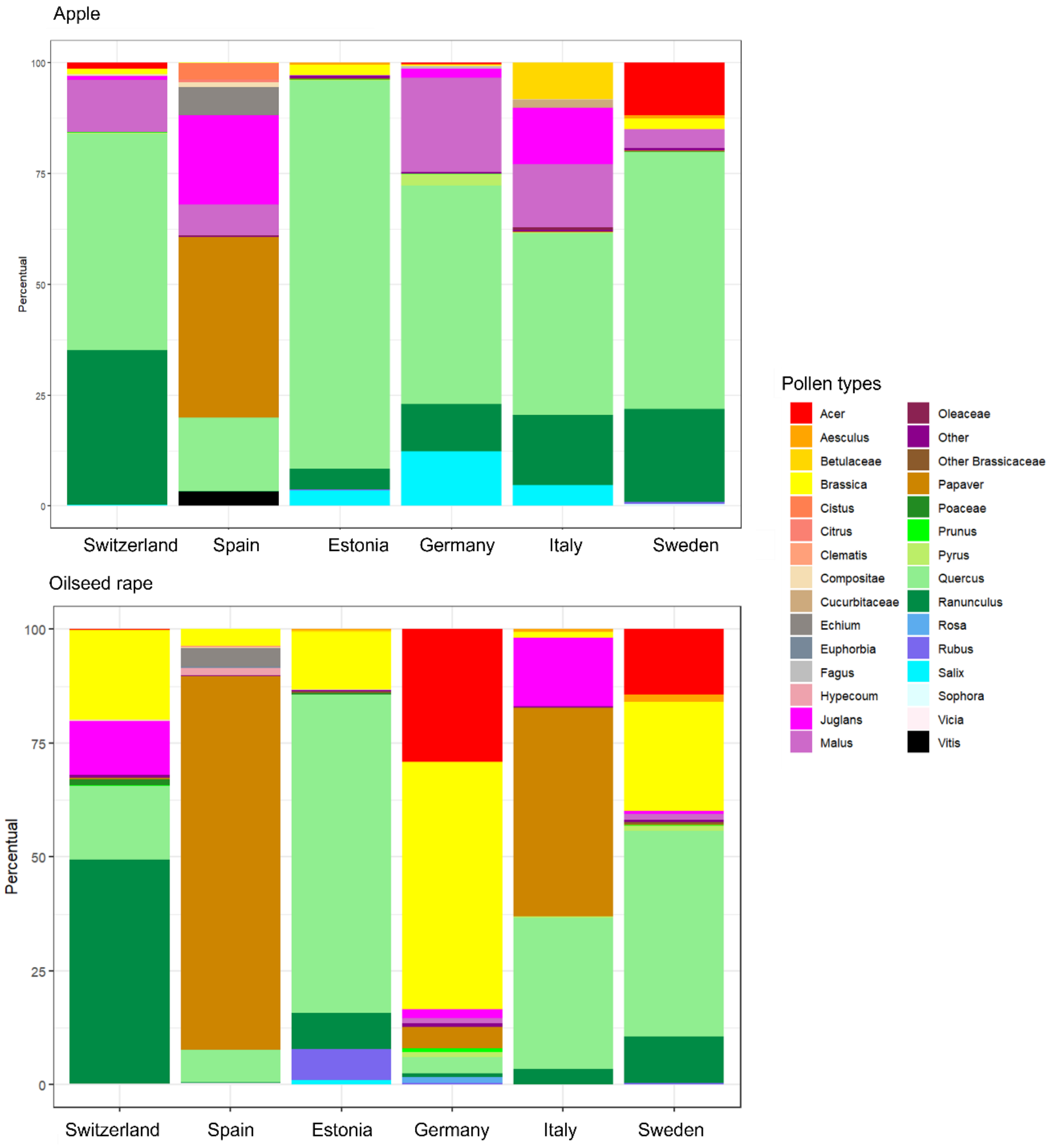

Figure 12. Pollen found in the nests in Apple (above) and oilseed rape (below) sites across the six countries. Graphs are only show those plant groups found in at least one site, greater than 0.5%.

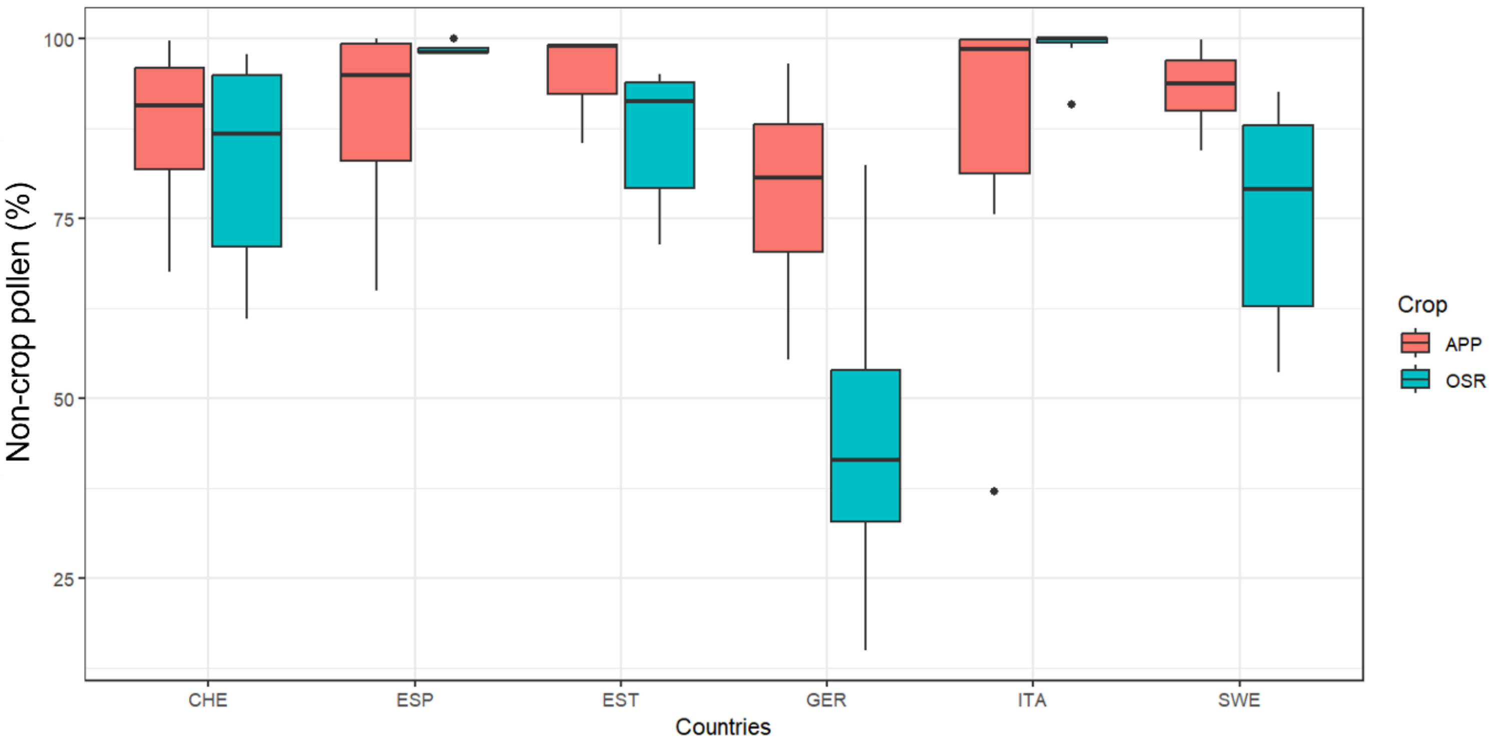

Figure 13. The proportion of non-crop pollen in apple (pink) and oilseed rape (blue) sites. Germany (GER) showed lower percentages of non-crop pollen in the stock compared with Spain (ESP), Estonia (EST) and Italy (ITA). No differences emerged in Switzerland (CHE) and Sweden (SWE).

4.4.2 Impact of the landscape on pollen stock and on the occupancy of the nests

Contrary to our hypothesis, there was no relationship between landscape composition and pollen diversity (Habitat diversity: *P*=0.57; Non-cultivated habitat (%): *P*=0.65; Crop (apple vs OSR): *P*=0.80 Tab. 6). On the other hand, and supporting our hypothesis, landscape was strongly related to the percentage of non-crop pollen present in the cells. Specifically, both habitat diversity and percentage of non-cultivated habitats were positively correlated with the percentage of non-crop pollen (respectively *P*<0.001 and *P*=0.005; Tab. 6; Fig. 14 A; Fig. 14 B), and there was less non-crop pollen in oilseed rape sites (*P*<0.001; Tab. 6; Fig. 14 C).

There was a higher rate of nest occupation in oilseed rape sites compared with apple orchards (*P*<0.001; Tab. 6; Fig. 15 A).

Table 6. Relationship between landscape variables (habitat diversity and % non-cultivated habitat) and pollen stocks, and nest occupancy. Asterisks indicate significant relationships (*** p< 0.001; ** p< 0.01).

Response Variable	Independent Variable	Estimate	Z-value	*P*
Pollen diversity	Habitat diversity	0.0714	0.574	0.566
	Non-cultivated (%)	-0.0015	-0.454	0.650
	Crop OSR	-0.0246	-0.264	0.792
Non-crop pollen (%)	Habitat diversity	0.5952	5.168	<0.001 ***
	Non-cultivated (%)	0.0086	2.799	0.0051 **
	Crop OSR	-0.3405	-4.318	<0.001 ***
Occupied cells	Crop OSR	1.8408	4.288	<0.001 ***

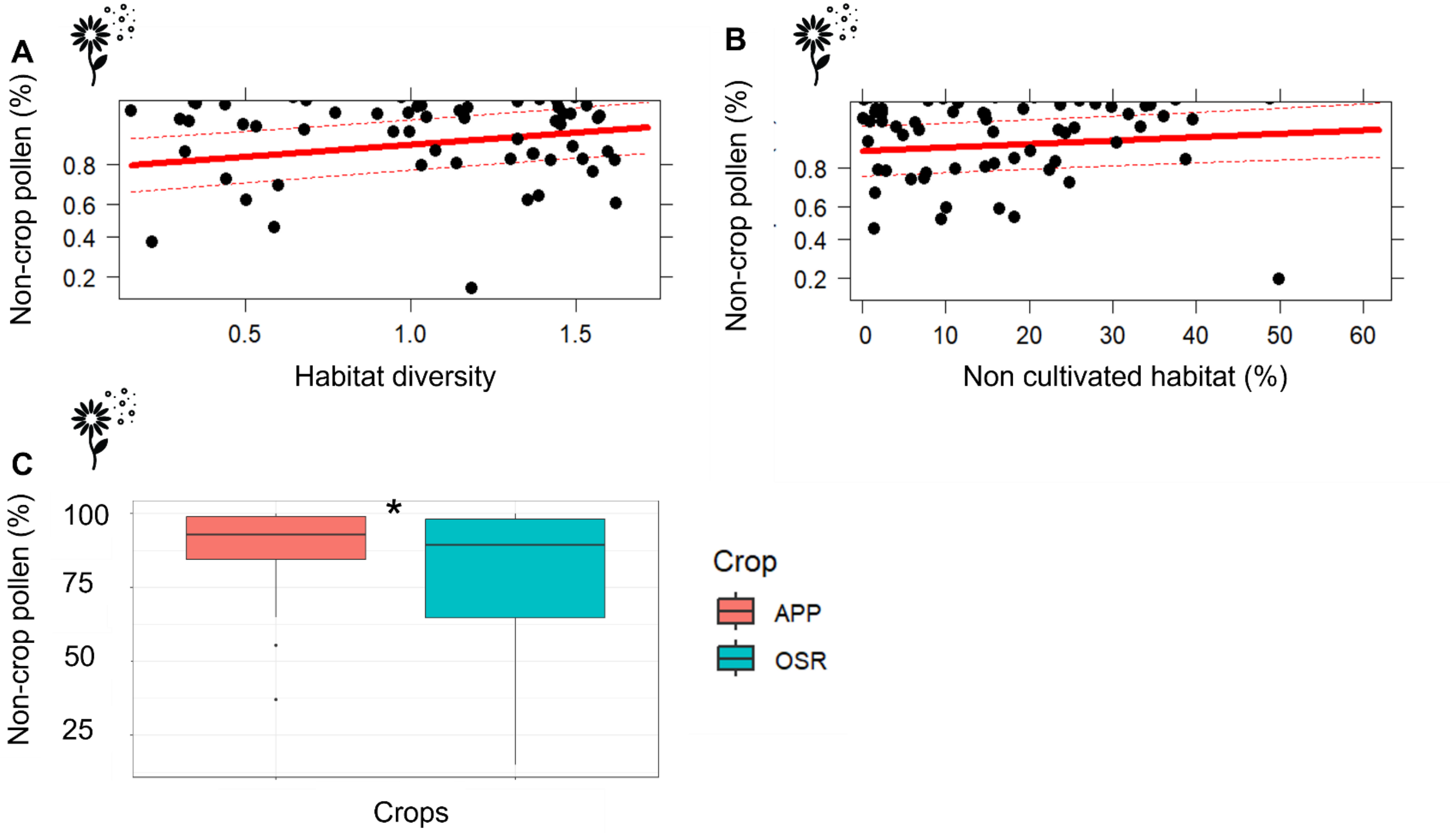

Figure 14. The relationship between habitat diversity (A), percentage of non-cultivated habitats (B), and crop type (C) and the percentage of non-crop pollen present in the pollen stock.

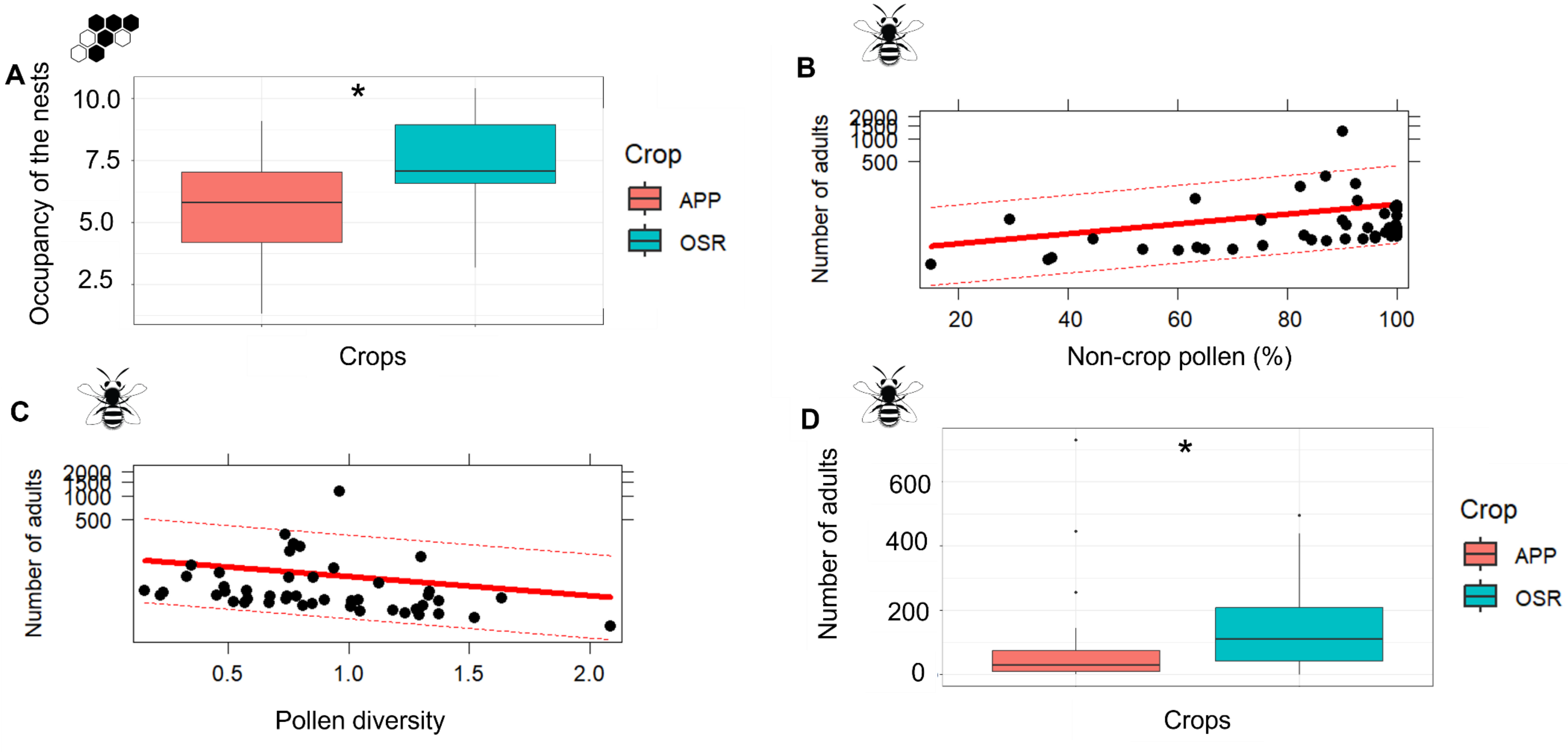

Figure 15. The number of occupied cells (A) and the number of adults (D) according to crop type (red = apple, blue = oilseed rape); and the relationship between the number of adults and the percentage of non-crop pollen (B) and pollen diversity (C).

4.4.3 Impact of the pollen stock on the life stages of *O. bicornis* bees

The percentage of non-crop pollen was positively related to the number of live adults that hatched from the nests (*P*<0.001; Tab. 7; Fig. 15 B). Contrarily, pollen diversity was negatively related to this parameter (*P*<0.001; Tab. 7; Fig. 15 C). More adults hatched from nests located in oilseed rape sites (*P*<0.001; Tab. 7; Fig. 15 D). Contrary to expectations, there was no relationship between pollen or the crop type and the rate of hatched pupae and on the mortality of larvae, nor on the sex ratio or the weight of the adults hatching the nests in spring 2020. The only exception was a negative relationship between the percentage of non-crop pollen and average female weight (*P*=0.037;Tab. 7).

Table 7. Relationship between pollen (diversity and % non-crop) and crop type, and the different life stages of *O. bicornis* bees. Asterisks indicate significant relationships (*** p< 0.001; * p< 0.05).

Response Variable	Independent Variable	Estimate	Z-value	*P*
Rate of hatched pupae	Pollen diversity	0.5164	0.496	0.62
	Non-crop pollen (%)	0.0078	0.433	0.665
	Crop OSR	0.6843	0.98	0.327
Alive Adults hatched	Pollen diversity	-0.6105	-14.498	<0.001 ***
	Non-crop pollen (%)	0.0165	19.757	<0.001 ***
	Crop OSR	0.2253	7.519	<0.001 ***
Sex ratio	Pollen diversity	0.1176	0.577	0.564
	Non-crop pollen (%)	-0.0017	-0.43	0.667
	Crop OSR	0.1239	0.794	0.427
Average weight of females	Pollen diversity	-0.305	-0.047	0.962
	Non-crop pollen (%)	-0.317	-2.088	0.03679 *
	Crop OSR	-0.978	-1.28	0.2004
Average weight of males	Pollen diversity	3.7184	0.636	0.5248
	Non-crop pollen (%)	-0.1476	-1.112	0.2663
	Crop OSR	-5.4728	-1.315	0.1884

4.5 Discussion

Our study investigated the relationship between the pollen stored in the nests (botanical origin and diversity) and the fitness of *O. bicornis*. In addition, we examined how landscape composition (habitat type and habitat diversity) modulates pollen provision. Previous studies showed *O. bicornis* collecting pollen from a wide range of species, but having a preference for specific types of non-cultivated plant pollen, that we also found highly represented in our pollen record (e.g. *Quercus* spp., *Ranunculus* spp., *Acer* spp., *Salix* spp., *Juglans* spp., *Papaver* spp.; Free & Williams, 1970; Tasei, 1973; Raw, 1974; Radmacher & Strohm, 2009; Coudrain et al., 2016; Bertrand et al., 2019). The nutritional composition of pollen had been found to affect mortality and growth of bees (Levin and Haydak, 1957; Roulston & Cane, 2000; Roulston & Cane, 2002; Praz et al., 2008).

Our findings offer new insights, suggesting that non-crop pollen might play an important role in increasing the overall fitness of *O. bicornis*, being positively related to higher numbers of adults emerging from the nests, a pattern that was consistent across a wide biogeographical range (Spain, Germany, Italy and Sweden). In addition, our results show that the percentage of non-crop pollen was positively modulated by the presence of non-cultivated and diverse habitats in the surrounding landscape (across all countries). Our results also showed that pollen diversity was negatively related with the number of adults hatched. These findings are supported by previous studies showing that the composition of the pollen stock, rather than its diversity, positively impacted populations of mason bees (Filipiak et al., 2019). More diverse pollen types do not necessarily reflect the dietary requirements of the bees and may limit the availability of some nutrients (such as P, Na, Mn, Mg, K, Fe, Ca, Zn and Cu; Filipiak et al., 2019) or contain secondary plant compounds, toxic for *O. bicornis* (Stevenson, 2020). Filipiak et al. (2002) found that some pollen types had suboptimal levels of some nutrients, for example oilseed rape pollen has low levels of Copper (Cu) and Sodium (Na). A lack of such elements can reduce *O. bicornis* fitness, increasing male mortality and reducing pupal development and mass, as well as the adult body mass in both sexes. However, Filipiak et al., (2002) also showed that supplementation of Cu and Na could remove or buffer such negative impacts. Thus, in habitats with limited plant species, dominated by mass-flowering crops like oilseed rape and other crops, the presence of non-crop pollen might buffer the effect of potential nutritional imbalances. Moreover, both low nutrient contents and the presence of toxic substances, associated with some plant species, can decrease bee fitness (Levin and Haydak, 1957; Stanley and Linskens, 1974; Roulston and Cane, 2000). Our results offer new insights by suggesting that non-crop pollen provided the larvae of *O. bicornis* with a better balance of nutrients necessary for them to develop, or to buffer potential nutritional shortfalls.

In the landscapes examined here, which were characterised by agricultural fields, the high diversity of pollen may be attributed to the presence of different crop types in addition to oilseed rape and apple, as well as wild plants. This could risk bees being exposed to pesticide residues, which can contaminate the nectar and pollen of a range of cultivated species (Radmacher and Strohm, 2009; Zioga et al. 2020; Bednarska et al., 2022). Zioga et al. (2020) reviewed pesticide residues in pollen and nectar and showed that pollen of crop origin had a higher concentration of active pesticide ingredients, compared with pollen from non-crop species. Consistent with this, in separate analyses (data not shown, but results and analyses reported in Appendix XVI a and XVI b), lower concentration of residues and a lower number of active ingredients were associated with increasing proportions of non-crop pollen in our sampling sites. The positive relationship between non-crop pollen and the number of adults emerging from the nests may be due to reduced pesticide exposure. Pesticides can have a negative impact on wild bee populations, diminishing their reproduction (Woodcock, 2017), increasing mortality of individuals subjected to pesticides via oral exposure (Mokkapati, 2021 a), or impacting the survival and development of larvae (Mokkapati, 2021 b). The fitness of *O. bicornis*, following pesticide exposure, can also diminish as a consequence of behavioural or physiological changes – e.g. differences in activities at the nest entrance and in flights after pesticide applications (Alkassab, 2020), lower immune-response (Brandt et al., 2020), or alteration of the energetic budget and metabolic rate (Mokkapati, 2022). The difference in the response of bees from oilseed rape sites compared with apple orchards (e.g in terms of the number of adult individuals), might be a result of the lower concentration of residues or the lower number of active ingredients detected in the pollen from nests located in oilseed rape fields (Appendix XVI a and XVI b), because of different application rates between the two crops, with more products used in apple orchards (Appendix XVI c). Further analyses are required to confirm our hypothesis, but other studies (Centrella et al., 2020) have shown an increase in risk to *O. bicornis* associated with fungicides, when pollen content of nests located in apple orchards contained more pollen of the Rosaceae family (which includes *Malus* spp.).

Besides the decrease of female weight, we found no effect of non-crop pollen on male weight, nor on any of the developmental stages of *O. bicornis*. However, body size and weight of *O. bicornis* are regulated by many environmental variables, therefore our results might reflect the impact of some variables that were not considered by this study. Previous studies suggested that the temperature that larvae were exposed to and the quantity of pollen stored in the nests (rather than pollen quality), influenced the weight of *O. bicornis* during different stages of development. Higher pollen provision positively impact on the weight of the hatched adults, but extreme temperatures decrease it (Wilcaniek et al., 2004; Radmacher and Strohm, 2009). Other factors impacting the body size of bees are related to the protein content of the pollen (Roulston et al. 2000). In addition, temperatures were also responsible for higher larvae mortality (Radmacher and Strohm, 2009). Further research on the larvae mortality, on the number of hatched pupae, and on the weight of the adults, is advised in order to identify possible lack of proteins in our record, or the co-occurrence of other environmental factors, that can impact on the different *O. bicornis* development.

Our results showed higher occupancy of the nests in those sites located in oilseed rape crops. A positive impact on nest building by *O. bicornis*, in relation to the extent of oilseed rape in the landscape, was already documented in Holzschuh et al. (2013). Our study further shows that more adults of *O. bicornis* emerged from those nests located in oilseed rape crops. These results considered together suggest a positive interaction between this type of crop and *O. bicornis* fitness. These correlations may indicate greater resources provided by this crop type to the bees or less exposure to pestices. Our study has found that bees collected more pollen of *Brassica* spp., rather than of *Malus* spp.. Previous studies showed that oilseed rape flowers produce more nectar per day, compared with apple flowers, and for this reason are considered highly attractive for some bee species (Nedić et al., 2013; Quinet et al., 2016; Carruthers et al., 2017) and in our study, there was greater extent (area) of oilseed rape crops in the landscape than apple orchards (see Appendix XII). Thus, in our study, oilseed rape crops may have provided overall more resources, compared with apple orchards, better supporting the *O. bicornis* aggregations. In fact, bees are central- place foragers needing foraging resources within the flight range of their nesting sites. The abundant food resources provided by oilseed rape crops close to the nests can promote short foraging flights, known to increase the fitness of bees, with repercussions on the sex ratio and on the parasite load in the cells (Orians and Pearson, 1979; Fryxell and Doucet, 1991; Frey-Roos etal., 1995; Ulbrich & Seidelmann, 2000; Bosch, 2008; Radmacher and Strohm, 2010). However, the sex ratio in our study was not related to any of the pollen or landscape features considered. Nevertheless, sex ratio can consistently change through time, with big fluctuations between years, probably due to changes in climate condition (Tepedino and Torchio, 1982). Assessing more than one year sampling and including data about the weather conditions during pupal development, might be useful to better investigate the role of pollen in determining the sex ratio of the adults hatched from the nests.

Ultimately, as expected, non-crop pollen increased with the percentage of non-cultivated and more diverse habitats surrounding the sites, indicating that such landscape characteristics might support *O. bicornis,* providing them with high quality pollen resources. Other studies have shown a positive relationship between the abundance and richness of bees, and the presence of forests in the landscape surrounding agricultural crops. Marini et al. (2012) showed that landscapes dominated by forests supported higher numbers of wild bee species in apple orchards than habitats dominated by grassland or orchards. Nagamitsu et al. (2018) showed that loss of natural forests in the landscape reduced the mass provision of pollen in the nests of mason bees. Hence, even though our results do not show a direct impact of non-cultivated habitats on *O. bicornis*, our findings stress the importance of preserving semi-natural and diverse areas to promote solitary bees fitness, providing more non-crop pollen for bees. Moreover, the presence of diverse habitats, other than agricultural landscape, supported higher percentages of non-crop pollen in the stock, probably because of the presence of habitats other than orchards and cultivated crops – e.g. grassland, meadows, woodlands and wetlands, or even urban areas. The latter are known as well for benefit wild bees, when they are managed without the use of pesticides and when the lawns are not mowed (Kaluza et al., 2016; Šlachta et al., 2020; Splitt et al., 2021).

4.5.1 Conclusion

Overall, our results show that non-cultivated habitats and flora benefit *O. bicornis,* through the provision of pollen with improved nutritional values (Filipiak et al. 2019), or with lower pesticides content (Radmacher and Strohm, 2009; Zioga et al. 2020; Bednarska et al., 2022). This is specifically true in those landscapes characterised by low floral composition and by the presence of agricultural crops. Moreover, our results show that within agricultural landscapes, crop type and its management impacted differently on the fitness of the bees – i.e. oilseed rape crops in our study seemed to have better supported *O. bicornis,* compared with apple orchards. This could be related to some preferences in the foraging behaviour or to differences in the area of the mass-flowering crops (Teper, 2007; Persson et al., 2018; Splitt et al., 2021; Ruddle et al., 2018), as well as to differences in pesticide application and concentration of residues (Centrella et al., 2020).

This study was intended to investigate at an European scale the relationship between the landscape composition and the pollen type (botanical origin and pollen diversity) on *O. bicornis* fitness. However, some countries did not manage to collect all the required information about the different bees developmental stages, given some difficulties in managing the aggregations of *O. bicornis,* limiting the information to a smaller subset of countries out of those initially selected. Nevertheless, we believe that our results offer new insights on the important role that non-cultivated habitats and non-crop pollen have at supporting *O. bicornis* aggregation in agricultural landscapes, across different biogeographic regions in Europe. However, future studies should extend the monitoring to more than one sampling season, for a better understanding of mechanisms regulating the *O. bicornis* population on a temporal-scale.

Ultimately, our results support the retention, or restoration, of non-cultivated elements (meadows, woodlands, shrubby areas, hedgerows, lines of trees and gardens) in the 1 km radius surrounding crops, to improve the quantity of non-crop pollen collected by *O. bicornis*. Where this is not possible, reducing the mowing of wild meadow patches in the vicinity of agricultural crops and preserving semi-natural features already present in the landscape. These measures would support higher abundance of *O. bicornis* in the crops, with benefits on the productivity of the fields, because this species has been found to pollinate both apple and oilseed rape crops (Jauker et al., 2012).

4.6 Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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CHAPTER 5

General Discussion

5. GENERAL DISCUSSION

5.1 Major findings

I aimed to investigate the impact of landscape composition and configuration, at different scales (field and 1 km radius scales) and in different biogeographic contexts, on five groups of flower-visiting insects. By analysing the abundance of pollinators commonly present in agricultural contexts across Europe, we can better understand the threats that are connected to landscape homogenisation. We investigated the direct impact of different landscape features on insect abundance, as well as the relationship between landscape and pollen, and how this can have repercussions on a solitary bee species common in Europe – *Osmia bicornis*. My main goal was to understand the role played by less-intensively managed habitats and non-crop habitats on the abundance of honey bees, bumble bees, solitary bees, hover flies and butterflies. My findings could contribute to increasing the level of understanding of pollinator status, to implementing or supporting agricultural policies already in force (Agri-Environmental Scheme – AES), and to suggesting new *ad hoc* projects related to different groups of insects in different agricultural habitats.

The composition of the habitats was the most incisive factor influencing the pollinator communities at a European scale, even though previous studies showed that also the spatial arrangement of crop fields and other habitats could promote insects in agroecosystems (Martin et al., 2019). My studies found that the abundance of insects in the two target agricultural crops (oilseed rape crops and apple orchards) were related to habitat diversity and to the presence and the extent of non-crop and less-intensively managed habitats, both at local and at 1 km radius scales. This was true for all three studies (Chapters 2-4), despite the non-crop habitats being constituted by different features. In Ireland, when comparing different locations in cultivated crops (Chapter 3), we found more hover flies and butterflies along the margins of the crops, compared with their centre. This was true in the apple orchards for the entire duration of the experiments (April-late August), and for both crops while they were in bloom, suggesting that flowered field margins provide fundamental food or nesting resources to some groups of insects. These results also suggest that flowering margins might provide alternative food resources to the main crop. Previous studies support these results showing wild flower strips to enhance species richness and abundance of wild bees (including Red List species) and to increase the number of species of butterflies (Buhk et al. 2018; Scheper et al. 2015). On the other hand, when the landscape was analysed across Europe at a 1 km radius (Chapter 2), a higher percentages of less-intensively managed and diverse habitats seemed to support insects in agricultural crops. Specifically, with increasing amounts of less-intensively managed habitats, including wetland habitats, commercial forestry, natural woodlands, managed grasslands for silage and pasture and semi-natural meadows, we found a higher abundance of the overall number of insects in oilseed rape crops, as well as a higher abundance of bumble bees and butterflies. Similarly, more diverse habitats were related to a higher abundance of hoverflies in apple orchards. Our results are supported by the literature, showing that hedgerows, meadows, grassland and forests support insect abundance in agricultural crops, providing both food and nesting resources and allowing the insects to move in the matrix (Marshall & Moonen, 2002; Rundölf et al., 2008; Marini et al.2012, Nayak et al., 2015; Nagamitsu et al., 2018; Raderschall et al., 2021; Martínez-Núñez et al., 2022).

My studies also show an indirect role of the habitats at shaping insects communities. Higher percentages of pollen of non-crop origin were found in those nests of *Osmia bicornis*, located in sites surrounded by abundant non-crop areas and by diverse habitats (Chapter 4). In this case, the non-crop areas were defined as natural woodlands, forestry, shrubby areas, hedgerows, lines of trees and gardens, at a 1 km radius. Because more adults hatched in those sites where a higher percentage of non-crop pollen was found, we assumed that non-crop habitats could indirectly support the fitness of *O. bicornis*. Thus, we suggest that non-crop pollen, provided by higher floral composition characterising the non-crop habitats, represents high quality pollen, maybe for its nutritionally balanced content (Filipiak et al., 2002) or because of its association with lower insecticide risk (Bednarska et al., 2022). Our results also suggest that the presence of trees and herbs characterising non-crop habitats could provide *O. bicornis* with the pollen of species that are preferred by these wild bees. In fact, our results showed, across all the countries, high percentages of *Quercus* spp., *Acer* spp., *Juglans* spp., *Salix* spp., *Papaver* spp., and *Ranunculus* spp. pollen, that are known for being the main components of *O. bicornis* diets (Free & Williams, 1970; Tasei, 1973; Raw, 1974; Radmacher & Strohm, 2009; Coudrain et al., 2016; Bertrand et al., 2019). I found that *Ranunculus* spp. was one of the main floral species along the margins of crops in Ireland during all three different periods of the year when the studies were conducted, (both during and after the flowering period of the target crops). This confirms that the role of natural elements, such as floral strips and trees in the landscape surrounding the agricultural crops and within agricultural crops themselves, could support insect groups across different temporal scales. These elements could fill nutritional gaps that were identified in an agricultural context at the end of the mass-flowering crops blossoming (Timberlake et al., 2019). These nutritional gaps are related to seasonal fluctuation of food resources, connected to the environment or to a lack of floral resources in some periods of the year (Scheper et al., 2015; Danner et al. 2016; Buhk et al. 2018; Timberlake et al., 2019; Russo et al., 2022). Nutritional gaps are correlated with low sugar provision not responding to the high energetic consumption demands of the insects (Ratnieks et al., 2014; Timberlake et al., 2019).

Nutritional gaps and lack of floral resources in agricultural landscape can also drive insect competition (Danner et al., 2016). In our study set in Ireland (Chapter 3), the number of honey bees present along the margins of the crops was constant across the three sampled periods, despite some beekeepers having moved hives to new sites once flowering ceased. This suggested that semi-natural features attract insects from the surrounding habitats, especially when food resources are scarce in the landscape, increasing the competition for food resources. Honey bees were consistently the most abundant taxon recorded (Chapter 2), possibly because of the presence of hives in the crops as part of the experimental set up, or installed by beekeepers and farmers to enable crop pollination (Hodge et al., 2022). Thus, there could be competition amongst species for semi-natural resources when food availability is limited (Danner et al., 2016). Enhancing the natural features in agricultural landscapes with floral resources characterised by different longevities and blooming times, might support different species during their life stages**,** and across the year (Danner et al. 2016; Buhk et al. 2018). On the other hand, enhancing semi-natural resources at a landscape scale can disperse insects in surrounding habitat, thus reducing competition (Veddeler, Klein & Tscharntke 2006; Holzschuh et al. 2011; Scheper et al., 2015).

Isolation was the only configurational landscape metric found to influence the abundance of flower-visiting insects (Chapter 2) and its effects were highly context-dependent. Previous studies analysing the responses of pollinators to edge density and semi-natural habitats, also reported non-linear responses across Europe and in different taxa. Those responses depended on the interaction of habitat configuration and composition (Martin et al., 2019). This suggests that adding some interaction terms in the mixed effect models, between habitat types and isolation, might provide more knowledge about the mechanisms guiding the insect responses. Moreover, the higher abundance of insects recorded on the field margins compared to the centre of the cultivation in Ireland, supports a role of these linear elements as compositional feature. If from one side, as already discussed, the field margins could provide food and nesting support, these elements can also be responsible for the movement between patches of the insects in the matrix (Bengtsson et al., 2005; Fahrig, 2003; Hole et al., 2005; Jonason et al., 2011; Marshall & Moonen, 2002).

Contrary to what we expected, the pollen and the plant diversity in our study did not show a positive correlation with the insect abundance in the agricultural fields. The abundance of bumble bees and hover flies were moderately correlated with the diversity of plants in Ireland, but conversely, the number of adult *O. bicornis* across Europe was negatively correlated with the pollen diversity. These results reveal the complexity of the mechanisms regulating plant-pollinator networks and that the quality and the composition of the pollen (and plants) rather than their diversity play a role in supporting insects groups (Bukovinszky et al., 2017; Filipiak et al., 2019). A greater plant diversity does not necessarily respond to the insects requirements, given differences in their diets and given differences in the nutritional content of different pollen types (Filipiak et al., 2019). In addition, previous studies showed that more diverse diets were also associated with higher levels of pesticide risk in the pollen collected by bees (Bednarska et al., 2022).

I found generally positive relationships between the percentage of less-intensively managed or non-crop areas and insect abundance, confirming that some types of cultivation can positively impact on some insect groups (Stanley and Stout, 2013; Holzschuh et al. 2013). Previous studies showed a positive role for oilseed rape crops in supporting solitary bee abundance, in some periods of the year (Holzschuh et al. 2013). The positive impact of these crops on insect abundance is probably due to highly rewarding flowering resources connected with these mass-flowering crops, at the time of their blossoming (Suzuki et al. 2009; Scheper et al. 2015). In our studies, more insects (with the exception of bumble bees) were recorded across Europe in those sites located in oilseed rape crops, rather than in apple orchards (Chapter 2). Similarly, *O. bicornis* nests located in oilseed rape crops were associated with higher rates of occupation and with more adults hatching (Chapter 4). However, some contradicting results emerged. The abundance of the solitary bees recorded across the Irish sites was higher in apple orchards, compared to oilseed rape crops (Chapter 3). Nevertheless, this effect was time-limited and only recorded during the first sampling period (April-May), while no differences were recorded later on in the season. This could be explained by the habitat surrounding the crops. Osterman et al., (2021) found more solitary bees in apple orchards surrounded by oilseed rape crops. Moreover, our results in Ireland could be related to the pooling of insects into the broad taxonomic group “wild bees”. Finer taxonomic scales analyses might confirm whether *O. bicornis* abundance is positively impacted by the presence of oilseed rape crops in Ireland. In fact, taxonomic differences in the responses to landscape characteristics can arise even within the same family or genus of insects, due to diverse food and nest requirements, or to the need for using several resources during their life cycle (Erhardt, 1985; Cane & Sipes, 2007; Erhardt & Mevi-Schütz, 2009; Meyer et al., 2009; Eckhardt et al., 2014; Bertrand et al., 2019).

Taxonomic differences were also confirmed in our studies when checking the responses of pollinators to agricultural habitats or to the temperature. When comparing the abundance of insects along the field margins and the centres of crops in Ireland, bumble bees and honey bees were the only groups whose abundance was found to be higher in the centre of the crop rather than along its margins (specifically in the apple orchards between April and May). Similar results were previously recorded for bumble bees in oilseed rape crops, comparing the field margins and the centre of the crops (Walther-Hellwig & Frankl, 2000). Actually, in our study investigating the impact of landscape composition and configuration on insect abundance across Europe, bumble bees positively responded to the number of mass-flowering crops and orchards adjacent to sites, unlike honey bees, hover flies and butterflies that showed negative trends. This confirms previous studies suggesting that some cultures can actually have a positive impact on the abundance of insects, probably because they provide abundant (despite limited in time) food resources and that such changes are taxon-specific (Westphal et al., 2003; Carrè et al., 2009; Suzuki et al. 2009; Holzschuh et al., 2012; Holzschuh et al., 2013; Stanley & Stout, 2013; Scheper et al., 2015; Timberlake et al., 2019). However, our results also showed that habitats characterised by extended areas devoted to orchard and urban settlement had a negative impact on insect abundance. Similar results are confirmed by the literature showing a negative impact of intensively managed areas with insect numbers (Potts et al., 2010 a; Goulson et al., 2015), even though the data related to urban areas are mixed (Theodorou et al. 2017).

5.2 Recommendations for management decisions

Overall, our results suggest a positive response to maintaining non-crop habitats and semi-natural features for supporting insect abundance in different types of agricultural contexts. Such features can be constituted by floral strips and hedgerows of non-cultivated plants in the immediate vicinity of the cultivated field, or by meadows. The introduction of native plants and flowers is a common technique used in agri-environment schemes to increase numbers and diversity of flower-visiting insects (e.g. Haaland et al., 2011; Campbell et al., 2017; Curtis et al., 2019; Heller et al., 2019). However, their value is highly taxonomic specific and landscape dependent (Campbell et al., 2017; Wix et al., 2019; Scheper et al. 2013). For this reason it is important to guarantee a certain level of variability of such semi-natural features, including different elements that might sustain different insect groups to better respond to their life cycle or diet/nesting requirement, or that might provide different resources at stages of the year (Maurer et al., 2022). Semi-natural elements such as, for example trees, should also be introduced in urban habitats in the vicinity of the cultivated crops, to ensure better feeding conditions (Splitt et al. 2021). However, both in agricultural contexts and in urban habitats, the introduction of semi-natural elements has to respect the habitats' characteristics and should involve the use of native species.

In addition, our studies show the potential role that some flower-visiting insects, other than managed species, can have on crops, given their abundance. In both Ireland and across Europe, hover flies were found to be the second most abundant group of insects after honey bees. This was true despite the presence of both honey bee hives and bumble bee nests set in the sites, whose presence was related to the co-occurrence of other experiments and to the use by farmers of these managed insects in crop pollination. Hover flies, for example, are known for providing several benefits to the crops (Doyle et al., 2020). Besides pollination (they visit 72% of global food crops; Rader et al., 2020; Doyle et al., 2020) they protect crops from pests and, because some of them are migratory species, they can transport pollen for long distances. High numbers of hover flies in oilseed rape and apple crops suggest that the pollination service of crops would be ensured even if honey bee hives would not be present. Similarly, Osterman et al., 2021, claimed that apple pollination would be ensured by wild bees, if honey bees are not present in the orchards, because distracted to other mass-flowering crops in the surrounding habitats. However, well-targeted floral resources are necessary to preserve wild bees in agricultural contexts (Russo et al., 2013). These results confirm the importance of preserving floral resources in cultivated crops and suggest that the presence of other species of insects, other than honey bees, could enable crop pollination. This suggests that the pollination service could be guaranteed in cultivation even with lower density beekeeping. Reduced numbers of hives would prevent foraging competition by honey bees. This could benefit both the local wild bees (higher occurrence and increased nectar foraging success), and honey bees (higher harvesting of nectar and pollen; Henry & Rodet, 2018).

5.3 Recommendations for future studies

Because different semi-natural elements can sustain different insect groups (Maurer et al., 2022) a detailed characterisation of "semi-natural habitats" could help to gather major information about the responses of the taxa to the landscape and as well as finding out what are the requirements they need to better survive in the agricultural context. Given the resolution of the habitat classification in our study, it was not possible to distinguish in detail which types of land-use constituted the less-intensive and non-crop habitats. Similarly it was not possible to separate highly managed grasslands (including pastures and silage fields) from semi-natural meadows, and commercial forestry from woodlands. Future studies should include such a level of identification of semi-natural habitats in their analyses.

Whilst I found a correlation between landscape composition and insect abundance, our results also show the importance of considering other factors in the analyses that can change both the insects' and the plants' composition. In the study we conducted in Ireland, seasonal shifts in the abundance of insects and in the abundance and diversity of plants were recorded, with separate assemblages of both insects and plants in the three different periods. This was not surprising and it could be attributed to normal phenological changes. However, in the study we conducted across Europe, we also found a strong impact of climate variables (annual temperature, annual precipitation and precipitation seasonality) on the abundance of insects. These results, concerning the role played by seasonal changes and climate parameters on shaping insects communities in cultivated crops, suggest that future studies should integrate timing and climatic analyses in their models. In addition, we believe that it would be useful to monitor the insects and plants phenology in relation to climate parameters, across several years, in order to identify possible fluctuations in their natural rhythms. This is important in the global context of climate change, where there is general concern about the impact that extreme temperatures or precipitation events could have, both on insects and plant communities, with a consequent disruption of the complex mechanisms regulating the plant-pollinator networks (Hegland et al., 2009; Grünewald et al. 2010; Potts et al., 2010 a; Goulson et al., 2015; Soroye et al. 2020).

5.4 Conclusion

The different responses that we obtained at the different scales and between the different groups of insects and crops types, highlight the need for more studies investigating on a wide scale the status of insects in Europe across different biogeographic ranges, through the adoption of common protocols. This would allow a deeper knowledge of the insects status in territories characterised by different climate conditions or landscape characteristics. In addition, a standardised approach could contribute to a better understanding of the threats that different taxa are facing and of the specific landscape requirements of different insects groups. This could contribute to create *ad hoc* policies for different regions and for different habitat types.

Our studies support the integration of semi-natural features in agricultural context to support insect communities, both at a crop scale – with the introduction of flowering hedgerow and wild floral resources constituted by native species along the margins of the crops – and on a 1 km radius scale around the cultivated crops – with the implementation of non-crop areas or less-intensively managed areas. These practices should follow the maintenance of semi-natural features already present in the landscape, whose presence depend on limiting the mowing of meadows and floral margins, limiting the clearance of the hedgerows, as well as limiting the use of plant protection products. Adoption of these measures and the preservation of non-crop features, would contribute to sustaining insects presence, abundance and richness in agricultural landscapes, thereby providing them with both high quality and abundant food resources, across different stages of their life cycles and helping them to move across the territory.

The consequences of these measures would also impact on the ecosystem on a wider scale, with repercussions for its conservation. Preserving insect presence in the cultivated crops would in fact enable and improve food production (Klein et al., 2007). In addition, their presence would contribute to maintaining plants biodiversity, since in Europe insects are responsible for pollinating over 80% of wild plants species (Potts, et al., 2010 b). Besides their role as pollinators, insects provide other ecosystem services, such as pest control, waste recycling (including dung burial), provisioning of food for several wild life animals (Losey & Vaughan, 2006). Increased biodiversity would provide better ecological services (such as the detoxification of chemicals, the recycle of nutrients in the ecosystem, pest control, water recycling of nutrients, regulation of microclimate and the reduction of flood risk; Altieri, 1999), ultimately contributing to having a more stable and resistant ecosystem, even in the context of climate change (Isbell et al., 2015).

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7. Appendices

Appendix I. The total number of transects performed in each crop in each of the different countries, with dates of first and last samples taken.

Country	Crop	Number of transects	First visit	Last visit
Switzerland (CHE)	Oilseed rape	31	23/04/2019	02/05/2019
Switzerland (CHE)	Apple	32	23/04/2019	25/04/2019
Spain (ESP)	Oilseed rape	96	29/04/2019	27/05/2019
Spain (ESP)	Apple	96	08/04/2019	17/05/2019
Estonia (EST)	Oilseed rape	64	13/05/2019	03/06/2019
Estonia (EST)	Apple	68	13/05/2019	03/06/2019
Great Britain (GBR)	Oilseed rape	96	20/04/2019	14/05/2019
Great Britain (GBR)	Apple	96	23/04/2019	10/05/2019
Germany (GER)	Oilseed rape	80	24/04/2019	13/06/2019
Germany (GER)	Apple	96	18/04/2019	06/05/2019
Ireland (IRE)	Oilseed rape	96	01/04/2019	13/05/2019
Ireland (IRE)	Apple	92	25/04/2019	07/06/2019
Italy (ITA)	Oilseed rape	96	15/04/2019	17/05/2019
Italy (ITA)	Apple	96	11/04/2019	14/05/2019
Sweden (SWE)	Oilseed rape	96	19/04/2019	03/06/2019
Sweden (SWE)	Apple	64	15/04/2019	01/06/2019

Appendix II. Description of all the landscape and climate variables used as independent variables in our initial analyses. The variables in black are those included in the final models; variables in grey are the ones that were not in any of the final models.

Type of variable	Independent variables	Description
LANDSCAPE COMPOSITION	**PLAND_Cropland**	**PLAND** is the proportion of the landscape belonging to class i. **Cropland** includes the cropland patches. **Orchards** include all the orchards patches (this parameter was considered only for the analyses tun for the apple sites) **SNH** defines the semi-natural patches (including Woodland –Woodlands, shrub plantations, hedgerows, lines of trees and gardens – and grassland – both meadows and pastures). **Urbanisation** includes Urban areas and Roads.
	PLAND_Orchard	
	PLAND_SNH	
	PLAND_Urbanisation	
	Landscape diversity (SHDI)	It is a widely used metric in biodiversity and ecology and takes both the number of classes and the abundance of each class into account. I t is calculated through the Shannon Diversity Index. $-\sum_{i=1}^{m}(Pi * lnPi)$
	Number of Adjacent mass-flowering crops	It shows the number of flowering crops adjacent to the main crop (our site). All the selected sites had 4 borders, so this value ranges from 0 (no mass flowering crops neighbouring with the sites) to 4 (all the adjacent fields are occupied by mass-flowering crops).
LANDSCAPE CONFIGURATION	**IJI**	Interspersion and Juxtaposition Index - It is a so called "salt and pepper" metric and describes the intermixing of classes (i.e. without considering like adjacencies - the diagonal of the adjacency table). The number of classes to calculate IJI must be ≥ than 3.
	NP_Cropland	Number of Patches - It describes the fragmentation of a class, however, does not necessarily contain information about the configuration or composition of the class.
	NP_Orchard	

LANDSCAPE CONFIGURATION	**ENN Cropland**	Coefficient of variation of Euclidean Nearest-Neighbour distance - It summarises each class as the Coefficient of variation of each patch belonging to class *i*. ENN measures the distance to the nearest neighbouring patch of the same class *i*. The distance is measured from edge-to-edge. The range is limited by the cell resolution on the lower limit and the landscape extent on the upper limit. The metric is a simple way to describe patch isolation. Values equal to 0 indicate that the Euclidean nearest-neighbour distance is identical for all patches. The values can increase, without limit, as the variation of ENN increases. Because it is scaled to the mean, it is easily comparable among different landscapes.
	ENN Orchards	
	ENN Semi-Natural patches	
CLIMATE and WEATHER	**Daily Temperature**	Temperature recorded at each visit to each site
	BIO_01	Annual mean temperature
	BIO_04	Temperature seasonality (standard deviation * 100)
	BIO_10	Mean temperature of the warmest quarter
	BIO_11	Mean temperature of the coldest quarter
	BIO_12	Annual precipitation
	BIO_15	Precipitation seasonality (coefficient of variation): proportion of the standard deviation of the total precipitation of the month over the average monthly total precipitation
	BIO_18	Precipitation of the warmest quartile
	BIO_19	Precipitation of the coldest quartile

Appendix III. Separate models were created for each of the groups of insects and for the two crops, depending on the AIC index. Subsequently, we “cleaned” each model in order to avoid any correlation between the variables (using a combination of hierarchical and correlative clusters, VIF analyses and AIC index). Using MuMIn function, the final model was selected. We ended up with different models for each insect group – the formulas show the models used for each analysis; the parameters written in grey show the variables that were eliminated during the process of obtaining the final models).

Analysed group	Model description
All taxa in apple	**glmer (pollinat_no_apis ~** proportion of Cropland + proportion of Urban + **proportion of Orchard** + proportion of Semi-Natural + Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural + Juxtaposition+ Landscape diversity + Annual Temperature + Temperature Seasonality + Mean Temperature warmest quartile + **Annual Precipitation +** Precipitation Seasonality + Precipitation warmest quartile + Adjacent mass-flowering crops + Daily Temperature + offset(log(n))+ Annual Temperature*Landscape diversity+ **(1|obs)** + (1|country)**, data= app, family = poisson (link = "log"))**
All taxa in OSR	**glmer (pollinat_no_apis ~** proportion of Cropland + proportion of Urban + **proportion of Semi-Natural +** Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity + **Annual Temperature +** Temperature Seasonality + Mean Temperature warmest quartile + **Annual Precipitation +** Precipitation Seasonality + Precipitation warmest quartile + Adjacent mass-flowering crops + **Daily Temperature +(1|obs) +offset(log(n))+** Annual Precipitation*Adjacent mass-flowering crops , **data= osr,family = poisson (link = "log"))**
Apis in Apple	**glmer (apis ~** proportion of Cropland + proportion of Urban + **proportion of Orchard +** proportion of Semi-Natural + Number patches Cropland + Isolation of Cropland + **Isolation of Orchard +** Isolation of Semi-natural +Juxtaposition+ Landscape diversity + Annual Temperature + Temperature Seasonality + Mean Temperature warmest quartile + **Annual Precipitation + Precipitation Seasonality** +Precipitation warmest quartile + Adjacent mass-flowering crops + Daily Temperature + **offset(log(n))+** Annual Temperature*Landscape diversity+ (1|country)+ **(1|obs), data= app, family = poisson (link = "log"))**
Apis in OSR	**glmer (apis ~** proportion of Cropland + proportion of Urban + proportion of Semi-Natural + Number patches Cropland + **Isolation of Cropland** + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity + Annual Temperature + Temperature Seasonality + Mean Temperature warmest quartile + Annual Precipitation + Precipitation Seasonality +Precipitation warmest quartile + **Adjacent mass-flowering crops + Daily Temperature + offset(log(n))+** Annual Temperature*Landscape diversity+ **(1|country)+ (1|obs), data= osr, family = poisson (link = "log"))**
Bombus spp. in Apple	**glmer (bombus ~** proportion of Cropland + proportion of Urban + **proportion of Orchard** + proportion of Semi-Natural + Number

	patches Cropland + Isolation of Cropland + Isolation of Orchard + **Isolation of Semi-natural** +Juxtaposition+ Landscape diversity + **Annual Temperature** + Temperature Seasonality + Mean Temperature warmest quartile + Annual Precipitation + **Precipitation Seasonality** +Precipitation warmest quartile + **Adjacent mass-flowering crops** + Daily Temperature + **offset(log(n))+** Annual Temperature*Adjacent mass-flowering crops + **(1|obs), data= app,family = poisson (link = "log"))**
Bombus spp. in OSR	**glmer (bombus** ~ proportion of Cropland + proportion of Urban + **proportion of Semi-Natural** + Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity **+ Annual Temperature** + Temperature Seasonality + Mean Temperature warmest quartile + Annual Precipitation **+ Precipitation Seasonality +** Precipitation warmest quartile + Adjacent mass-flowering crops + Daily Temperature + **offset(log(n))+** Annual Precipitation*Adjacent mass-flowering crops+ **(1|obs), data= osr, family = poisson (link = "log"))**
Solitary bee in Apple	**glmer (solitary** ~ proportion of Cropland + proportion of Urban + **proportion of Orchard** + proportion of Semi-Natural + Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity + **Annual Temperature** + Temperature Seasonality + Mean Temperature warmest quartile **+ Annual Precipitation** + Precipitation Seasonality +Precipitation warmest quartile + Adjacent mass-flowering crops + Daily Temperature + **offset(log(n))**+ Annual Precipitation*Adjacent mass-flowering crops+ (1|country)+**(1|obs), data= app, family = poisson (link = "log"))**
Solitary bee in OSR	**glmer(solitary ~** proportion of Cropland + proportion of Urban + proportion of Semi-Natural + Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ **Landscape diversity** + **Annual Temperature** + Temperature Seasonality + Mean Temperature warmest quartile + **Annual Precipitation** + Precipitation Seasonality +Precipitation warmest quartile + Adjacent mass-flowering crops + **Daily Temperature** + **offset(log(n))+ Annual Temperature*Landscape diversity+** (1|country)+ **(1|obs), data= osr, family = poisson (link = "log"))**
Hover flies in Apple	**glmer (hover flies** ~ proportion of Cropland + **proportion of Urban** + proportion of Orchard + proportion of Semi-Natural + Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ **Landscape diversity** + Annual Temperature + Temperature Seasonality + Mean Temperature warmest quartile + Annual Precipitation + Precipitation Seasonality +Precipitation warmest quartile + Adjacent mass-flowering crops + Daily Temperature + **offset(log(n))**+ Annual Precipitation*Adjacent mass-flowering crops+ (1|country)+ **(1|obs), data= app, family = poisson (link = "log"))**
Hover flies in OSR	**glmer(hover flies** ~ proportion of Cropland + proportion of Urban + proportion of Semi-Natural + Number patches Cropland + Isolation of Cropland + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity + **Annual Temperature** + Temperature Seasonality + Mean Temperature warmest quartile + Annual Precipitation + Precipitation Seasonality Precipitation warmest quartile + **Adjacent mass-flowering crops** + Daily Temperature + **offset(log(n))**+ Annual Precipitation*Adjacent mass-

	flowering crops+ (1|country) **+(1|obs), data= osr, family = poisson (link = "log"))**
Lepidoptera in Apple	**glmer (lepidoptera ~** proportion of Cropland + proportion of Urban + proportion of Orchard + proportion of Semi-Natural + Number patches Cropland + **Isolation of Cropland +** Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity + Annual Temperature + Temperature Seasonality + Mean Temperature warmest quartile + Annual Precipitation + **Precipitation Seasonality +** Precipitation warmest quartile + **Adjacent mass-flowering crops** + **Daily Temperature +(1|obs)+ offset(log(n))+** Annual Precipitation*Adjacent mass-flowering crops , **data= app, family = poisson (link = "log"))**
Lepidoptera in OSR	**glmer (lepidoptera ~** proportion of Cropland + proportion of Urban + **proportion of Semi-Natural** + Number patches Cropland + **Isolation of Cropland** + Isolation of Orchard + Isolation of Semi-natural +Juxtaposition+ Landscape diversity + **Annual Temperature +** Temperature Seasonality + Mean Temperature warmest quartile + **Annual Precipitation +** Precipitation Seasonality + Precipitation warmest quartile + Adjacent mass-flowering crops + **Daily Temperature** + **offset(log(n))**+ Annual Precipitation*Adjacent mass-flowering crops+ **(1|obs), data= osr, family = poisson (link = "log"))**

Appendix IV. Summary of study site Information including area, crop density main crop variety, and dates related to flowering period and pollinator surveys. Actual site locations cannot be given due to GDPR. (Boundary types: H-hedge; T-trees;W-wall; N-no physical boundary)

					Boundary type					Period 1		Period 2		Period 3	
Crop	Site	Location (County)	Area (ha)	Grassland (%; 1 km radius)	1	2	Date sown	Flowering started	Flowering ended	1st Visit	2nd Visit	1st Visit	2nd Visit	1st Visit	2nd Visit
OSR	1	Meath	19	43	HT	H	14.08.18	07.03.19	25.05.19	21.04.19	24.04.19	22.06.19	27.06.19	04.08.19	06.08.19
	2	Meath	22	48	HT	HT	14.08.18	10.03.19	31.05.19	11.04.19	21.04.19	22.06.19	27.06.19	01.08.19	06.08.19
	3	Kildare	0.5	18	W	W	30.09.18	20.03.19	30.05.19	01.04.19	10.04.19	26.06.19	29.06.19	08.08.19	13.08.19
	4	Kildare	5	20	H	H	21.08.18	12.03.19	02.06.19	11.04.19	21.04.19	22.06.19	27.06.19	01.08.19	02.08.19
	5	Laois	10	28	H	N	21.08.18	07.03.19	30.05.19	01.04.19	10.04.19	01.07.19	02.07.19	02.08.19	07.08.19
	6	Louth	10	31	H	H	14.08.18	14.03.19	30.05.19	22.04.19	25.04.19	24.06.19	28.06.19	03.08.19	04.08.19
APP	7	Tipperary	3.5	62	T	T	-	06.04.19	28.05.19	16.05.19	28.05.19	01.07.19	02.07.19	08.08.19	13.08.19
	8	Offaly	0.9	76	N	W	-	16.04.19	16.05.19	16.05.19	29.05.19	26.06.19	29.06.19	01.08.19	02.08.19
	9	Dublin	0.4	52	HT	HT	-	10.04.19	31.05.19	04.05.19	15.05.19	24.06.19	28.06.19	04.08.19	07.08.19
	10	Dublin	2.4	36	T	HT	-	06.04.19	26.05.19	04.05.19	11.05.19	24.06.19	28.06.19	03.08.19	07.08.19
	11	Meath	4.0	15	HT	T	-	06.04.19	26.05.19	25.04.19	06.05.19	24.06.19	28.06.19	03.08.19	04.08.19

Appendix V. A) Results of REML analyses (*P* values) examining the response of insect abundance and pollinator diversity to crop type (APP v OSR) and location (crop centre v field margin) during the main crop flowering period. B) Results of REML analyses (*P* values) examining the response of insect abundance and pollinator diversity to location (crop centre v field margin) and study period considering only the insects recorded in the apple sites. C) Results of REML analyses (*P* values) examining the response of insect abundance and pollinator diversity to crop type (APP v OSR) and study period considering the insects in both crops but only in the field margins. n.d.f. – numerator degrees of freedom. Analyses were conducted in R studio using the function lme (package "lme4" Bates et al. 2015).

When comparing the following results with those reported in the manuscript (analyses performed in Genstat v19 software) no differences emerge. The only exception appears in the REML analyses (*P* values) examining the response of insect richness to study period, in the apple sites (B). The difference can be attributed to the different type of data we used in the analyses – the current insect data were not square root transformed.

A)

	Crop type	Location	Interaction
n.d.f.	1	1	1
Apis mellifera	0.608	0.102	0.219
Bombus	0.588	**0.030**	**0.014**
Butterflies	0.760	**0.031**	0.155
Solitary bees	0.055	0.379	0.483
Syrphids	0.380	**0.028**	0.717
Total	0.715	0.457	**0.035**
Richness	0.348	0.063	0.859
Diversity	0.156	0.201	0.733

B)

	Period	Location	Interaction
n.d.f.	2	1	2
Apis mellifera	**0.036**	0.631	**0.004**
Bombus	0.386	0.210	**0.018**
Butterflies	**0.029**	**0.018**	0.123
Solitary bees	**0.015**	0.209	0.420
Syrphids	**0.002**	**<0.001**	0.307
Total	0.197	0.334	**0.002**
Richness	**0.029**	**<0.001**	0.213
Diversity	**0.071**	**0.001**	0.264

C)

	Crop type	Period	Interaction
n.d.f.	1	2	2
Apis mellifera	0.728	0.113	0.457
Bombus	0.143	0.476	0.591
Butterflies	0.228	**<0.001**	0.793
Solitary bees	0.474	**0.024**	0.114
Syrphids	0.309	**<0.001**	0.385
Total	0.285	0.143	0.888
Richness	0.451	0.462	0.723
Diversity	0.449	0.349	0.692

Appendix VI. Results of REML repeated measures analysis (*P*-values) examining the effects of crop type (apples/ OSR) and period (flowering period/ 1-month after flowering period / 3-month after flowering period) on abundance and diversity of flowering plants in the field boundary. Site was included in the REML model as a random factor. n.d.f. – numerator degrees of freedom; d.d.f – denominator degrees of freedom. Analyses were conducted in R studio using the function lme (package "lme4" Bates et al. 2015).

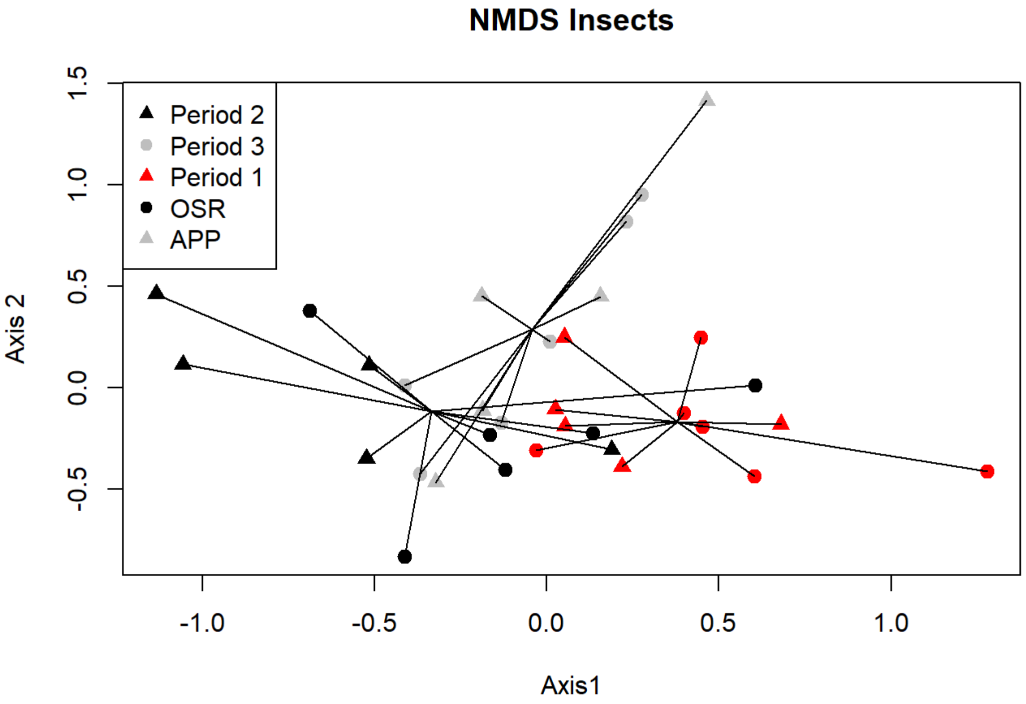
	Crop type	Period	Interaction
n.d.f.	1	2	2
d.d.f.	9	18	18
Median abundance	0.137	**0.002**	0.272
Total species richness	0.610	**0.005**	0.373
Diversity	0.414	**<0.001**	0.068

Appendix VII. Spearman's rank correlation coefficients (r_S) showing strength and direction of relationships between attributes of pollinating insect assemblage and diversity and abundance of flowering plants in field boundaries during 3 site visits. [Critical values of r_S with $n = 33$, $P < 0.05$ |0.356|** and $P < 0.1$ |0.301|*]. Analyses were performed in R studio, using the function "cor.test" in the package "ggpubr".

		Floral variables		
		Median abundance	Flower diversity *H*	Flower richness *S*
Insect variables	*Apis mellifera* abundance	0.153	0.151	0.176
	Bombus abundance	0.197	0.355**	0.228
	Solitary bee abundance	0.292	0.184	0.197
	Syrphid abundance	0.196	0.337*	0.328*
	Butterfly abundance	-0.134	-0.327*	-0.394**
	Total abundance	0.290	0.365**	0.301*
	Insect *S*	0.167	0.248	0.179
	Insect *H*	0.056	0	-0.026

Appedix VIII A) NMDS plot based on abundance of five groups of pollinating insects occurring in field margins in apple orchards (APP) and OSR during the main crop flowering (Period), 1-month after flowering (Period 2) and 3-months after flowering (Period 3). The permutation analysis of variance (PERMANOVA) showed an impact of the period (B), but not of the crop type (C) on the shift of the insect community. The asterixis indicates significative results related to the H0 hypothesis (*** *P*< 0.001).

A)



B)

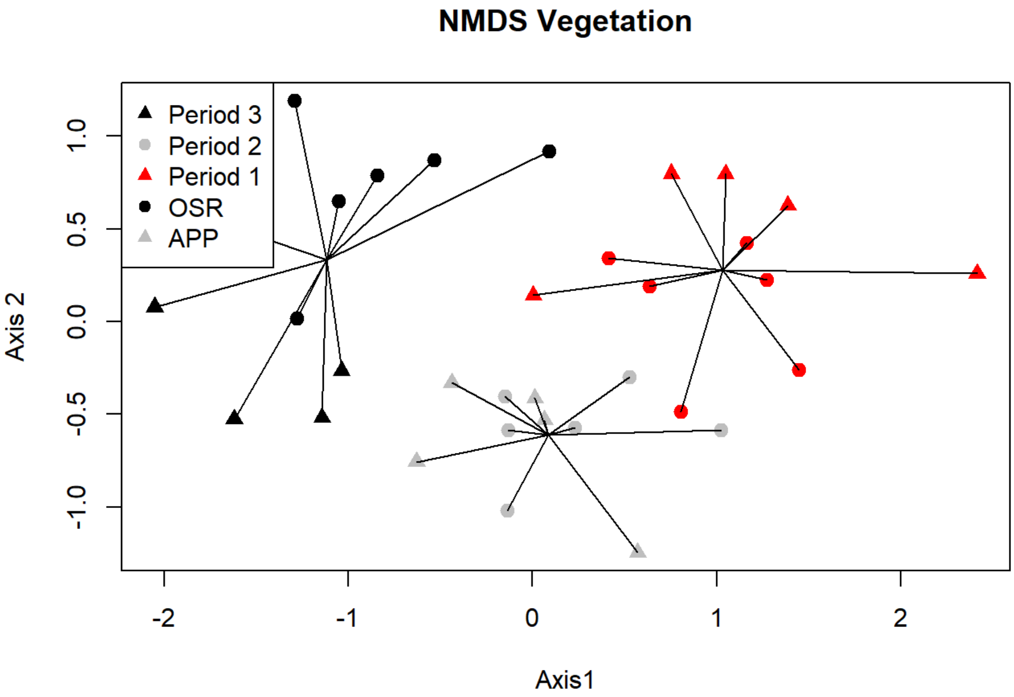
	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Period	2	1.3953	0.69763	4.3994	0.22678	0.001***
Residuals	30	4.7572	0.15857		0.77322	
Total	32	6.1524			1.00000	

C)

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Crop	1	0.2780	0.27798	1.4669	0.04518	0.174
Residuals	31	5.8745	0.18950		0.95482	
Total	32	6.1524			1.00000	

Appedix IX. A) NMDS plot based on frequency of field boundary flowering plants occurring in field margins in apple orchards (APP) and OSR during the main crop flowering (Period), 1-month after flowering (Period 2) and 3-months after flowering (Period 3). The permutation analysis of variance (PERMANOVA) showed an impact of the period (B), and of crop type (C) on the shift of the insect community. However, differences related to the crop type only emerged in some periods (A, D). The asterixis indicates significative results related to the H0 hypothesis (*** *P*< 0.001; ** *P*< 0.01; * *P*<0.05; **.** *P*<0.1).

A)



B)

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Period	2	3.6325	1.81625	5.8593	0.2809	0.001***
Residuals	30	9.2993	0.30998		0.7191	
Total	32	12.9318			1.0000	

C)

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Crop	1	0.744	0.74403	1.8925	0.05753	0.026*
Residuals	31	12.188	0.39315		0.94247	
Total	32	12.932			1.00000	

D)

	Df	SumsOfSqs	MeanSqs	F.Model	R2	Pr(>F)
Crop	1	0.7440	0.74403	2.6020	0.05753	0.003 **
Period	2	3.6325	1.81625	6.3517	0.28090	0.001 ***
Crop:Period	2	0.8348	0.41740	1.4597	0.06455	0.055 .
Residuals	27	7.7205	0.28594		0.59702	
Total	32	12.9318			1.00000	

Appendix X. Abundance of A. butterflies and B. bumble bees in OSR crops and Apple orchards, in Period 1 (April-May), Period 2 (June-July) and Period 3 (August), in field margins (FM) and centres of crops (CC)

A.

Crop	OSR				Apples						Total
Period	1	1	2	3	1	1	2	2	3	3	
Position	CC	FM	FM	FM	CC	FM	CC	FM	CC	FM	
Aglais io	1	1		5					1	2	10
Aglais urticae	1	5					1		1		8
Anthocaris cardamine		12				4					16
Aphantopus hyperantus				1							1
Celastrina argiolus				1							1
Coenonympha pamphilus			2								2
Lasiommata megera										1	1
Leptidae spp.										1	1
Lycaena phlaeas	1		1								2
Maniola jurtina								1		2	3
Pararge aegeria	1	1	2	2	3	1	1	3	2	2	18
Pieris spp.		10	3	43	3	5			6	13	83
Polyommatus icarus		1		4						2	7
Pyronia tithonus				3							3
Vanessa atlanta					2					1	3
Vanessa cardui			1	1					1	2	5
Unknown		2				1					3

B.

Crop	OSR				Apples						Total
Period	1	1	2	3	1	1	2	2	3	3	
Position	CC	FM	FM	FM	CC	FM	CC	FM	CC	FM	
B. hortorum		1			2	2		2			7
B. jonellus			1					1			2
B. lapidarius	23	26	12	5	7					4	77
B. pascuorum	3	8	19	15	5	9		14	2	6	81
B. pratorum			1	2	4	1	1	4		2	15
B. terrestris/lucorum agg.	41	39	72	45	73	16	26	30	59	30	431
Unknown	2				2						4

Appendix XI. List of field margin plant species recorded in each crop in each period.

	OSR Period 1	APP Period 1	OSR Period 2	APP Period 2	OSR Period 3	App Period 3
Alliaria petolata	✓					
Anthriscus sylvestris	✓	✓	✓			
Arum maculatum		✓				
Bellis perennis		✓		✓		✓
Brassica napus	✓					
Buddleja davidii						✓
Capsellabursa pastoris	✓					
Cardamine pratensis	✓	✓				
Cerastium arvense	✓					
Cerastium fontanum	✓	✓		✓		
Chamaemelum nobile				✓		✓
Cirsium arvense						✓
Cirsium vulgare			✓		✓	
Crataegus monogyna	✓	✓		✓		
Crepis capillaris						✓
Epilobium ciliatum				✓		
Epilobium hirsutum			✓		✓	✓
Epilobium montana						✓
Euphorbia helioscopa	✓					
Ficaria verna		✓				
Filipendula ulmaria					✓	
Fumaria muralis	✓					
Fumaria officinalis	✓					
Fumaria spp.	✓					
Galium aparine			✓	✓		
Geranium colombinum			✓		✓	
Geranium robertianum	✓		✓	✓	✓	
Geranium spp.						✓
Heracleum sphondylium			✓	✓	✓	
Hirschfeldia incana			✓			
Hyacinthoides hispanica		✓				
Hyacinthoides spp.		✓				
Jacobea vulgaris						✓
Labium hybridum	✓					
Lapsana communis			✓		✓	✓
Lapsana spp.						✓
Linum bienne			✓			
Lotus corniculatus						✓
Lysimachia arvensis			✓			
Malus pumila		✓				
Malus spp.		✓				
Matricaria discoidea	✓					
Matricaria recutita				✓		
Medicago lupulina	✓				✓	✓
Myosotis arvensis			✓	✓	✓	✓

Myosotis scorpioides		✓				
Nasturtium spp.						✓
Papaver dubium				✓		
Papaver rhoeas			✓		✓	
Papaver spp.	✓					
Poa annua	✓					
Polygonum maculosa					✓	
Prunella vulgaris				✓		✓
Ranunculus repens		✓	✓	✓	✓	✓
Raphanus raphanistrum			✓			
Rosa canina			✓	✓		
Rubus fruticosus			✓	✓	✓	✓
Rumex obtusifolius			✓	✓		✓
Sambucus nigra		✓	✓	✓		
Senecio vulgare	✓		✓			
Sinapis arvensis	✓					
Sisymbrium officinale	✓					
Smyrnium olosatrum		✓				
Solanum dulcamara					✓	
Sonchus asper			✓			✓
Sonchus oleraceus	✓					
Stachys palustris					✓	
Stellaria media				✓		
Taraxacum officinale	✓	✓				✓
Torilis japonica					✓	
Trifolium repens			✓	✓		
Ulex europaeus	✓					
Urtica dioca			✓	✓		
Urtica spp.			✓	✓	✓	✓
Veronica chamaedris				✓		
Veronica persica	✓					✓
Viburnum davidii		✓				
Viburnum opulus		✓				
Vicia cracca			✓	✓		
Vicia sativa		✓				
Vicia sepium	✓	✓	✓	✓	✓	
Viola tricolor	✓					

Appendix XII. The dates of the installation of the *Osmia bicornis* nests in the field preceded of a few days the starting date of the oilseed rape and apple flowers. The area of each field is indicated in hectares. The average area of apple orchards was 5.88 ha, while the average area of oilseed rape crops was 21.13 ha. The minimum and maximum areas of the crops were respectively 0.32 ha and 45 ha (for apple) and 0.96 ha and 135 ha (for oilseed rape).The countries are indicated with their labels – CHE, Switzelrland; ESP, Spain; EST, Estonia; GER, Germany; ITA, Italy; SWE, Sweden. The missing data are indicated with a dash (-).

Country	**Crop type**	**Site**	**Area (ha)**	**Date flowering started**	**Date flowering ended**	**Date Osmia installed**
CHE	OSR	1	1.0	14/04/2019	19/05/2019	11/04/2019
CHE	OSR	2	1.2	14/04/2019	20/05/2019	11/04/2019
CHE	OSR	3	2.0	14/04/2019	25/05/2019	11/04/2019
CHE	OSR	4	1.3	18/04/2019	21/05/2019	11/04/2019
CHE	OSR	5	5.5	19/04/2019	27/05/2019	11/04/2019
CHE	OSR	6	2.6	19/04/2019	25/05/2019	11/04/2019
CHE	OSR	7	2.1	14/04/2019	21/05/2019	12/04/2019
CHE	OSR	8	2.4	19/04/2019	25/05/2019	12/04/2019
CHE	APP	9	1.4	16/04/2019	11/05/2019	12/04/2019
CHE	APP	10	1	16/04/2019	11/05/2019	12/04/2019
CHE	APP	11	0.5	17/04/2019	08/05/2019	12/04/2019
CHE	APP	12	2	16/04/2019	12/05/2019	12/04/2019
CHE	APP	13	2.5	17/04/2019	14/05/2019	12/04/2019
CHE	APP	14	3.3	17/04/2019	14/05/2019	12/04/2019
CHE	APP	15	4.5	17/04/2019	16/05/2019	12/04/2019
CHE	APP	16	0.5	17/04/2019	19/05/2019	12/04/2019
ESP	OSR	1	24.7	07/04/2019	30/05/2019	16/04/2019
ESP	OSR	2	33.0	07/04/2019	30/05/2019	16/04/2019
ESP	OSR	3	19.5	10/04/2019	30/05/2019	16/04/2019
ESP	OSR	4	29.6	13/04/2019	30/05/2019	16/04/2019
ESP	OSR	5	40.0	13/04/2019	30/05/2019	16/04/2019
ESP	OSR	6	8.4	07/04/2019	30/05/2019	16/04/2019
ESP	OSR	7	7.0	10/04/2019	30/05/2019	16/04/2019
ESP	OSR	8	26.5	10/04/2019	30/05/2019	16/04/2019
ESP	APP	9	0.54	25/03/2019	15/05/2019	28/03/2019
ESP	APP	10	0.35	15/04/2019	15/05/2019	28/03/2019
ESP	APP	11	5.63	18/04/2019	20/05/2019	28/03/2019
ESP	APP	12	9.2	25/03/2019	15/05/2019	28/03/2019
ESP	APP	13	0.87	08/04/2019	20/05/2019	28/03/2019
ESP	APP	14	1.46	25/03/2019	15/05/2019	28/03/2019
ESP	APP	15	0.5	08/04/2019	20/05/2019	28/03/2019
ESP	APP	16	0.32	15/04/2019	20/05/2019	28/03/2019
EST	OSR	1	29.0	12/05/2019	31/05/2019	10/05/2019
EST	OSR	2	129.5	17/05/2019	04/06/2019	10/05/2019
EST	OSR	3	-	14/05/2019	01/06/2019	10/05/2019
EST	OSR	4	55.0	12/05/2019	31/05/2019	12/05/2019
EST	OSR	5	14	16/05/2019	02/06/2019	12/05/2019
EST	OSR	6	-	-	-	10/05/2019

EST	OSR	7	7.38	17/05/2019	03/06/2019	12/05/2019
EST	OSR	8	8.3	12/05/2019	01/06/2019	10/05/2019
EST	APP	9	12.30	16/05/2019	28/05/2019	12/05/2019
EST	APP	10	10.00	18/05/2019	29/05/2019	12/05/2019
EST	APP	11	1.34	16/05/2019	30/05/2019	10/05/2019
EST	APP	12	40.00	16/05/2019	30/05/2019	10/05/2019
EST	APP	13	12.29	12/05/2019	26/05/2019	12/05/2019
EST	APP	14	2.20	22/05/2019	03/06/2019	12/05/2019
EST	APP	15	7.00	13/05/2019	28/05/2019	12/05/2019
EST	APP	16	8.50	18/05/2019	30/05/2019	10/05/2019
GER	OSR	1	53.0	15/04/2019	05/06/2019	17/04/2019
GER	OSR	2	18.0	15/04/2019	05/06/2019	17/04/2019
GER	OSR	3	135.0	15/04/2019	05/06/2019	17/04/2019
GER	OSR	4	10.0	15/04/2019	05/06/2019	17/04/2019
GER	OSR	5	51.9	15/04/2019	05/06/2019	18/04/2019
GER	OSR	6	90.0	15/04/2019	05/06/2019	18/04/2019
GER	OSR	7	25.2	15/04/2019	05/06/2019	17/04/2019
GER	OSR	8	25.0	15/04/2019	05/06/2019	17/04/2019
GER	APP	9	7.55	18/04/2019	05/05/2019	15/04/2019
GER	APP	10	2.13	19/04/2019	06/05/2019	15/04/2019
GER	APP	11	2.00	19/04/2019	06/05/2019	15/04/2019
GER	APP	12	1.50	19/04/2019	06/05/2019	15/04/2019
GER	APP	13	0.62	18/04/2019	05/05/2019	15/04/2019
GER	APP	14	1.79	19/04/2019	06/05/2019	15/04/2019
GER	APP	15	1.69	19/04/2019	06/05/2019	15/04/2019
GER	APP	16	2.45	19/04/2019	06/05/2019	15/04/2019
ITA	OSR	1	2.3	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	2	1.4	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	3	2.3	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	4	7.4	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	5	16.4	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	6	1.7	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	7	1.0	15/04/2019	19/05/2019	15/04/2019
ITA	OSR	8	2.0	15/04/2019	19/05/2019	15/04/2019
ITA	APP	9	1.39	11/04/2019	11/05/2019	11/04/2019
ITA	APP	10	0.37	12/04/2019	11/05/2019	12/04/2019
ITA	APP	11	0.6	11/04/2019	15/05/2019	11/04/2019
ITA	APP	12	2.36	12/04/2019	11/05/2019	12/04/2019
ITA	APP	13	1.65	11/04/2019	15/05/2019	11/04/2019
ITA	APP	14	0.39	12/04/2019	15/05/2019	12/04/2019
ITA	APP	15	0.51	11/04/2019	11/05/2019	11/04/2019
ITA	APP	16	0.59	12/04/2019	11/05/2019	12/04/2019
SWE	OSR	1	9.0	01/05/2019	10/06/2019	28/04/2019
SWE	OSR	2	15.0	-	-	27/04/2019
SWE	OSR	3	9.0	-	-	27/04/2019
SWE	OSR	4	10.0	-	-	27/04/2019
SWE	OSR	5	12.5	-	-	27/04/2019
SWE	OSR	6	15.0	-	-	28/04/2019
SWE	OSR	7	6.0	-	-	28/04/2019
SWE	OSR	8	3.2	-	-	28/04/2019
SWE	APP	9	26	-	-	03/05/2019
SWE	APP	10	4	10/05/2019	25/05/2019	02/05/2019
SWE	APP	11	45	-	-	03/05/2019
SWE	APP	12	1.5	-	-	03/05/2019

SWE	APP	13	3	10/05/2019	23/05/2019	03/05/2019
SWE	APP	14	25	05/05/2019	25/05/2019	02/05/2019
SWE	APP	15	14	15/05/2019	25/05/2019	03/05/2019
SWE	APP	16	8	01/05/2019	15/05/2019	03/05/2019

Appendix XIII. Scheme illustrating the activities performed for the protocol. In the photo is shown the model of the nests used in the field.

Each nest has 100 cardboard tubes, filled with 100 pupae. Sex ratio 1:1 Pupae stored ar 2°C

For 2-3 weeks pupae stored at 12 °C to break diapause

3-7 days before flowering periods (spring 2019) 3 nests are set in each site facing South

At the peak of flowering period **10 tubes per site were collected** and sent to the labs for palynological analyses

At the end of the flowering period a mesh was placed on the nests to exclude further bees and enemies

For at least 4 weeks nests were left in the fields for larvae to develop

Trap nests collected from the fields snd stored outdoors **for 4 more months (until late September-mid October)**

In **October** 2019 mesh remouved the mesh. The **seasled and unsealed tubes were counted**, as well as the **parasitoids** leaving the nests

30 cardboards were remouved from each site to record the number of **cells containing only pollen, dead larvae, pupae**

Hibernation of the remaining tubes at lab conditions (2°C and 60-80% humidity) until March 2020

End of hybernation after keeping the tubes at 10 °C and 60-80% humidity

Emerging speciments are collected and **adult bees** and **parasitoids** counted. **Weight and sex** of bees was recorded

Appendix XIV. Pollen grains from different plant types found in the *O. bicornis* nests. Botanical origin is given as crops or not (wild pollen), herbaceous or woody and total number of grains.

Pollen type	**Pollen plant origin**	**Herbaceous or Woody**	**Total Number of Pollen grains in all samples**
Acer	Non-crop	Woody	2139
Aesculus	Non-crop	Woody	172
Allium f.	Non-crop	Herbaceous	3
Amaranthaceae	Non-crop	Herbaceous	2
Anchusa/Pulmonaria	Non-crop	Herbaceous	1
Apiaceae	Non-crop	Herbaceous	2
Betulaceae	Non-crop	Woody	270
Brassica f.	Cultivated	-	4504
Brassicaceae <20 µm	Non-crop	Herbaceous	40
Buddleja	Non-crop	Woody	1
Caprifoliaceae	Non-crop	Woody	1
Caryophyllaceae	Non-crop	Herbaceous	2
Cistus	Non-crop	Woody	145
Citrus	Cultivated	-	27
Clematis	Non-crop	Woody	28
Compositae	Non-crop	Herbaceous	86
Coronilla/Hippocrepis	Non-crop	Herbaceous	3
Crataegus	Non-crop	Woody	1
Cucurbitaceae	Non-crop	Herbaceous	56
Echium	Non-crop	Herbaceous	417
Ericaceae	Non-crop	Woody	3
Euphorbia f.	Non-crop	Herbaceous	10
Fagus	Non-crop	Woody	21
Forsythia f.	Non-crop	Woody	7
Fragaria/Potentilla	Non-crop	Herbaceous	5
Fraxinus	Non-crop	Woody	11
Genista f.	Non-crop	Woody	1
Geraniaceae	Non-crop	Herbaceous	1
Gleditsia	Non-crop	Woody	1
Hypecoum	Non-crop	Herbaceous	65
Ilex	Non-crop	Woody	3
Juglans	Non-crop	Woody	2411
Labiatae	Non-crop	Herbaceous	7
Lamium	Non-crop	Herbaceous	3
Ligustrum f.	Non-crop	Woody	10
Limonium	Non-crop	Herbaceous	1
Lonicera	Non-crop	Woody	3
Lotus	Non-crop	Herbaceous	1
Malus f.	Cultivated	-	2061

Oleaceae	Cultivated	-	22
Papaver	Non-crop	Herbaceous	6958
Phacelia	Non-crop	Herbaceous	4
Photinia	Non-crop	Woody	7
Pinaceae	Non-crop	Woody	25
Plantago	Non-crop	Herbaceous	3
Poaceae	Non-crop	Herbaceous	60
Poterium	Non-crop	Herbaceous	6
Prunus f.	Non-crop	Woody	43
Pyrus f.	Non-crop	Woody	226
Quercus	Non-crop	Woody	17666
Ranunculus f.	Non-crop	Herbaceous	5283
Rhamnaceae	Non-crop	Woody	1
Robinia	Non-crop	Woody	19
Rosa f.	Non-crop	Woody	46
Rubus f.	Non-crop	Woody	333
Rumex	Non-crop	Herbaceous	3
Salix	Non-crop	Woody	825
Sambucus nigra	Non-crop	Woody	10
Scrophulariaceae	Non-crop	Herbaceous	2
Sinapis f.	Non-crop	Herbaceous	9
Sophora	Non-crop	Woody	16
Tamarix	Non-crop	Woody	7
Thalictrum	Non-crop	Herbaceous	5
Unknown	Unknown	Unknown	8
Urticaceae/Cannabaceae	Non-crop	Herbaceous	5
Vicia	Non-crop	Herbaceous	28
Viola	Non-crop	Herbaceous	3
Vitis	Cultivated	-	131

Appendix XV. Parameters measured in each crop type in each country. The number of occupied cells was recorded across all the countries, but the other parameters were not. The dark grey bars show for a specific country and crop type the corresponding data collected.

Data	Estonia		Germany		Italy		Spain		Sweden		Switzerland	
	Apple	OSR	Apple	OSR	Apple	OSR	Apple	OSR	Apple	OSR	Apple	OSR
Number of occupied cells	■	■	■	■	■	■	■	■	■	■	■	■
Rate of mortality	■	■		■	■	■	■	■	■	■		
Alive Adults hatched				■	■	■	■	■	■	■		
Sex ratio				■	■	■	■	■	■	■		
Average weight of females				■			■	■	■	■		
Average weight of males				■			■	■	■	■		
Parasitoids				■	■	■			■	■		

Appendix XVI. Relationship between the percentage of wild pollen present in the stock and of crop types, on a) the number of active ingredients groups detected, and on **b**) the overall quantity (concentration) of residues, in the pollen collected by *O. bicornis*. The results **a**) are obtained by analysing the impact of crop type and percentage of wild pollen present in the pollen stock on the number of active ingredients found in the pollen, with the use of mixed effect models with poisson distribution (package glmmTMB in R studio), using the country as a random effect. The results reported in c) were obtained with the use of mixed effects model where the quantity of product applied overall in the sites (number of time the product was sprayed and its quantity) was analysed in relation to the type of crop (apple and oilseed rape), using the country as a random effect. Analyses on the collinearity between variables (check_collinearity function in package) and of the residual check (simulateResiduals function DHARMA package) were run to assess the reliability of the model. The asterixis indicates significative results related to the H0 hypothesis (*** $P< 0.001$; ** $P< 0.01$).

a)

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	18.53988	2.78342	6.661	2.72e-11 ***
Non-crop	-0.08241	0.02755	-2.991	0.00278 **
CropOSR	-4.96381	0.88258	-5.624	1.86e-08 ***

b)

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	12.9902292	0.5719907	22.7	<2e-16 ***
Non-crop	-0.0657172	0.0001587	-414.1	<2e-16 ***
CropOSR	-3.5456823	0.0111691	-317.5	<2e-16 ***

c)

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.15707	0.32663	9.666	<2e-16 ***
CropOSR	-0.90132	0.06229	-14.469	<2e-16 ***