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

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Introduction: 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 analyzed 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.

Methods: 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).

Results: 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 hover fly 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, particularly bumble bees and butterflies. 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.

Discussion: Thus, in the context of global change, our findings emphasize 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.

KEYWORDS

habitat heterogeneity, intensity gradient of land-use, pollinators, standardized approach, European biogeographic regions

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 and 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, 2011; Warren et al., 2021), and over one-third of the European hover fly species are threatened as well (IUCN–International Union for Conservation of Nature, 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; Winfree et al., 2009; Potts et al., 2010; Scheper et al., 2013; 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 characterized 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 and 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; Steffan-Dewenter and Tscharntke, 1999; Gathmann and Tscharntke, 2002; Hadley and Betts, 2012).

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 (Steffan-Dewenter et al., 2002; Rundlöf et al., 2008a; Cranmer et al., 2012; Kennedy et al., 2013; Bourke et al., 2014). 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 (Marshall and Moonen, 2002; Fahrig, 2003; Bengtsson et al., 2005; Hole et al., 2005; Jonason et al., 2011). Mass-flowering crops can also be attractive to flower-visiting insects, by offering food resources with short-term beneficial effects for pollinators (Westphal et al., 2003; Jauker et al., 2012; Holzschuh et al., 2016), while floral strips, hedges, bushes and field margins can fill

nutritional gaps outside the blooming periods of these crops (Timberlake et al., 2019; Bottero et al., 2021).

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, behavior, floral resource preferences and, nesting, and overwintering sites (Gathmann and Tschardt, 2002; Fenster et al., 2004; Cane et al., 2006; Klein et al., 2012). A recent meta-analysis analyzing 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 (Vicens and Bosch, 2000; Brittain et al., 2013; Lawson and Rands, 2019; Martinet et al., 2021), with consequent cascading impacts on plant-pollinator interactions (Hegland et al., 2009; Vasiliev and 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 hypothesized 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 hypothesized 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.

Methods

Experimental design

Eight countries were selected within the PoshBee site network (<https://poshbee.eu/>; Figure 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 to encompass 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 (Figure 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 center 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). A significant confounding factor in these studies was the presence of three honey bee (*Apis mellifera*) colonies and three bumble bee (*B. terrestris*) colonies in each site, and three *Osmia bicornis* trap nests in some of the sites, at the time of sampling – as sentinel colonies for other studies conducted at the same time in the PoshBee site network (Hodge et al., 2022). These sentinel colonies were introduced to the landscape immediately prior to blooming and removed immediately afterwards (Hodge et al., 2022), and thus will not have had long-term effects in the local pollinator community composition. However, they might have contributed to the insect survey data for these three pollinator groups. The statistical section describes how these biases were addressed during the analyses.

Insect surveys

We recorded the presence of 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 transects were placed in the center of the focal crop field or orchard and two along the respective margins. The two transects in the center of the crops were at least 30 m apart, at least 30 m from the edges of the field and as close as possible to the center 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 analyze variation within the crop field. Each transect was 50 m long and 2 m wide and walked for 5 min 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; see Supplementary Table S1). Insect surveys were only performed during suitable weather conditions, and between 10.00 am and 4.00 pm (see Mahon and Hodge, 2022). Due to unfavorable weather conditions or the difficulties accessing the center 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.

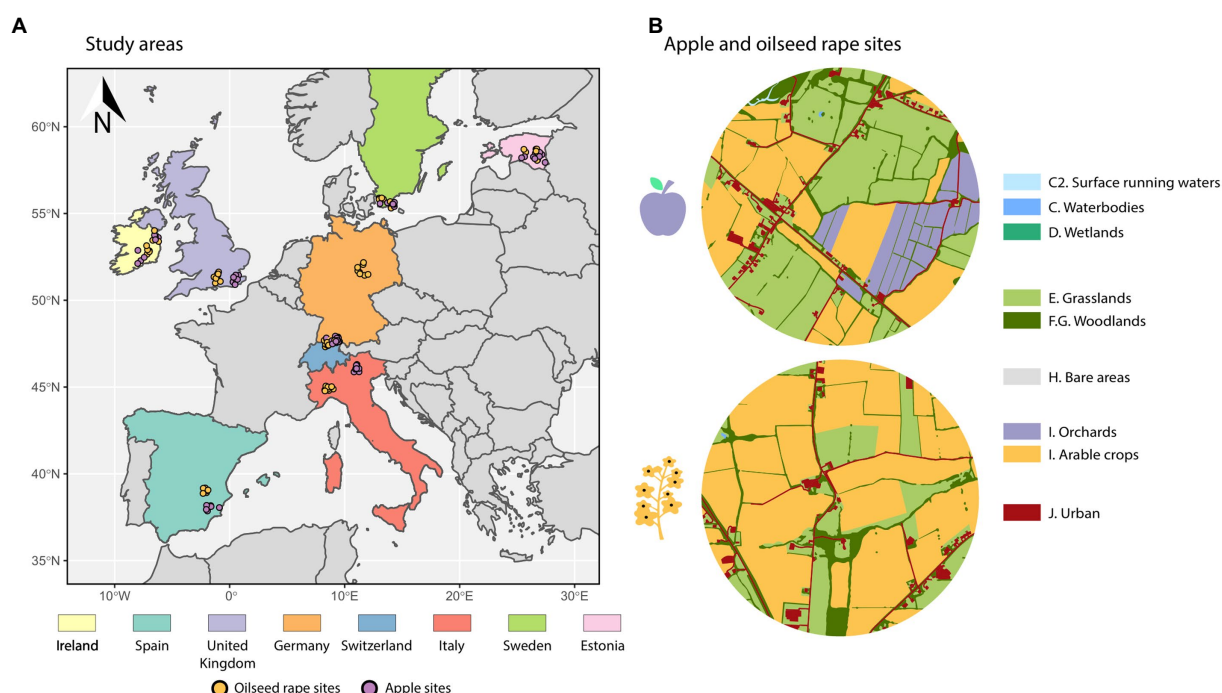


FIGURE 1

(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.

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 (Figure 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 Figure 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 and Moonen, 2002; Marini et al., 2012a; Alison et al., 2022). 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; Supplementary Table S2). 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 (see Supplementary Table S2). 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 (Supplementary Table S2). 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-Neighbor 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).

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 (Supplementary Table S2). For each site, long-term climate parameters (30 years averages from 1970 to 2000, spatial resolution approximately 1 km²), 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 and Hijmans, 2017; Supplementary Table S2).

Statistical analyses

The impacts of landscape structure, weather and climatic conditions on the abundance of the different insect groups were assessed using generalized linear mixed effects models (GLMM) with a Poisson distribution and a logit link, using country as a random factor (Supplementary Table S3). Because of the disparity in the insect surveys performed between countries (Supplementary Table S1), we pooled insect count data per site and used the number of visits to each site as an offset in the GLMMs.

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 (Hodge et al., 2022), we did not directly compare the different groups of insects in an overall model. 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 removed *A. mellifera* counts from the “total Insects” group because of their high abundance in the samples (72%; Figure 2), boosted by three sentinel honey bee colonies nearby and the pervasive presence of beekeeping in many of the landscapes. The remaining 28% of the Total Insects record was split more-or-less evenly between hover flies, butterflies, bumble bees and solitary bees, including possible contributions by the two other experimentally placed sentinel bee species (*B. terrestris* and *O. bicornis*). 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 (Supplementary Table S3). 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 (Supplementary Table S2).

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). If the

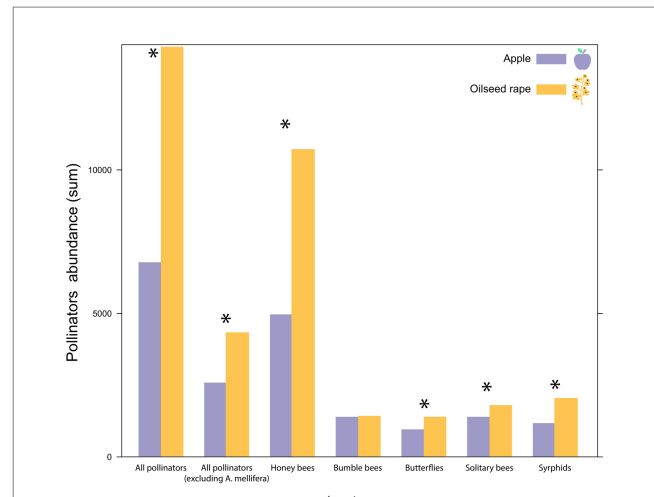


FIGURE 2

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.

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 and 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 generalized 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 and Weisberg, 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).

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; Figure 2). Honey bees (*A. mellifera*) were by far 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; Figure 2). 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; Figure 2), 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; Figure 2). Total insect abundances and abundances of all taxonomic groups were significantly higher in oilseed rape sites than in the apple sites (all $p < 0.001$; Figure 2), except for bumble bees ($p = 0.6$; Figure 2). The extent to which the survey records were augmented by the sentinel honey bee colonies and *O. bicornis* trap nests at the center of the sites is not known. Wild and feral colonies of the bee species are also very common throughout the biogeographic range covered by the sites (hence their choice as sentinel species) and indistinguishable from sentinel-derived bees. However, since the number of bees in these sentinel colonies was rigorously standardized across sites prior to placement (Hodge et al., 2022), the numerical basis for their presence in the survey records is essentially identical for the sites. The actual presence of sentinel bees in the survey records is therefore primarily subjected to the same landscape and climate factors as their wild conspecifics, for the purpose of statistical analysis. Of course, any beekeeping around each of the 128 sites may have biased the number of non-sentinel honey bees at the sites, as function of the number of colonies within range, augmented by social recruitment to the site's focal crop in competition with other floral resources: factors that are neither known nor can be modelled reliably. For this reason honey bees are analyzed separately throughout the study.

Landscape composition

At the field scale, the responses of insects to the number of mass-flowering crops adjacent to the site were taxon-specific (Figure 3). Bumble bee abundance was positively correlated with the extent of mass-flowering crops and orchards surrounding the apple sites ($p < 0.001$; Tables 1, 2; Figure 3). However, both honey bees and hover flies abundance was negatively correlated with mass-flowering crops and orchards surrounding the oilseed rape sites (respectively $p = 0.01$ and $p < 0.001$; Tables 1, 2; Figure 3). Butterfly abundance in the apple sites showed a moderate decline with the increase of mass-flowering crops and orchards in the surrounding landscape ($p = 0.07$; Tables 1, 2).

A high proportion of orchards in the landscape surrounding the apple sites was negatively correlated with total insect abundance (excluding honey bees; $p < 0.001$; Tables 1, 2; Figure 3), bumble bees ($p < 0.001$; Tables 1, 2) and solitary bees ($p < 0.001$; Tables 1, 2). Honey bees were slightly more abundant in sites surrounded by a higher proportion of orchards, although this result was not statistically significant ($p = 0.08$; Tables 1, 2). Beekeeping is popular near fruit orchards, both for hobby and for pollination services, and could well have generated this marginal effect. The proportion of urban area negatively influenced hover flies in the apple sites ($p = 0.02$; Tables 1, 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 ($p = 0.002$; Tables 1, 2; Figure 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; Tables 1, 2).

High landscape diversity in the surrounding landscape increased the abundance of hover flies ($p = 0.02$; Tables 1, 2). Solitary bees were also positively influenced by landscape diversity, although this was only found in oilseed rape sites ($p = 0.09$; Tables 1, 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 ($p < 0.001$; Tables 1, 2). On the other hand, isolation of orchard patches was negatively correlated with the abundance of honey bees in apple sites ($p = 0.01$ Tables 1, 2). Honey bees in oilseed rape sites showed a positive correlation with the isolation of cropland patches ($p < 0.001$; Tables 1, 2). A positive relationship between the isolation of cropland and butterflies was also found in apple sites ($p < 0.001$; Tables 1, 2; Figure 3). However, the opposite was found for butterflies in oilseed rape sites, where abundance declined with increasing isolation of cropland patches ($p = 0.04$; Tables 1, 2; Figure 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 (Tables 1, 2; Figure 3).

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

By analyzing 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 $p = 0.003$, $p = 0.004$, $p = 0.02$; Tables 1, 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 $p = 0.02$; Tables 1, 2), whereas the abundance of bumble bees was negatively correlated with annual temperature in both crop types ($p < 0.001$; Tables 1, 2; Figure 3). Moreover, a positive interaction of annual temperature and landscape diversity on the abundance of solitary bees in oilseed rape sites was found ($p = 0.002$; Table 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 (Tables 1, 2). The abundance of honey bees and solitary bees in apple sites were positively correlated with increasing annual precipitation ($p < 0.001$; Tables 1, 2). On the

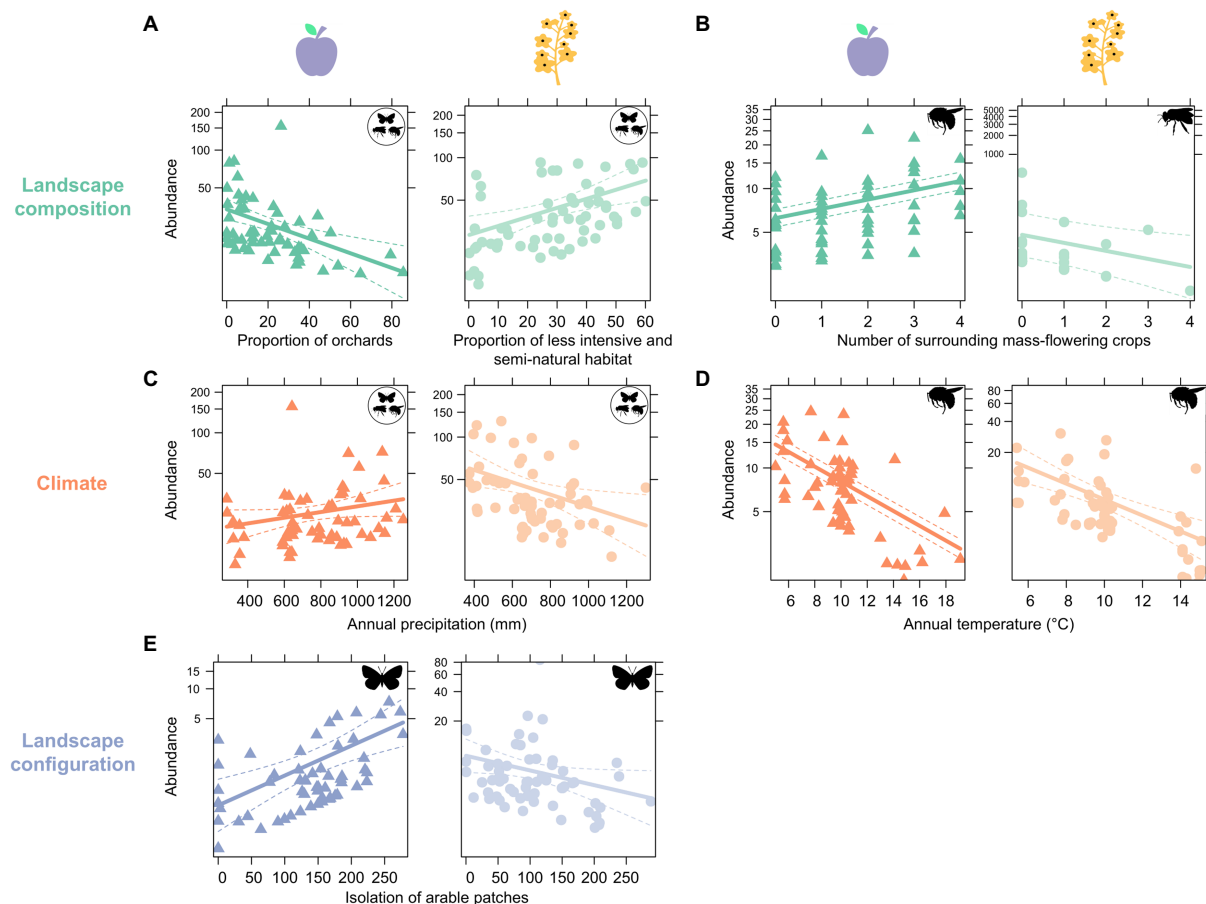


FIGURE 3

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.

other hand, solitary bee and butterfly abundances in oilseed rape sites responded negatively to annual precipitation (respectively $p = 0.002$ and $p < 0.001$; Tables 1, 2). Finally, precipitation seasonality was negatively correlated with the abundance of bumble bees in both apple and oilseed rape sites ($p < 0.001$ and $p = 0.02$; Tables 1, 2), although it was positively associated with the abundance of honey bees and butterflies in apple sites ($p < 0.001$; Tables 1, 2).

Discussion

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), our analyses only considered insect abundance in very broad taxonomic categories. While previous studies found hover flies 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 hover flies and solitary bees (Stanley et al., 2013), we were not able to investigate species-level patterns, except for honey bees.

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 and Stout, 2013). However, bumble bees also include other plant 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; Burns and Stanley, 2022; Gamonal Gomez et al., 2023). 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

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).

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***
		<i>A. mellifera</i>	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***
		Hover flies	0.2646	0.1139	2.323	0.02*
Landscape diversity (SHDI)	APP	Solitary bees	0.2531	0.1504	1.683	0.09
Isolation of orchard patches	APP	<i>A. mellifera</i>	−0.2430	0.0966	−2.516	0.01*
Isolation of cropland patches	APP	Butterflies	0.5331	0.1412	3.776	<0.001***
		<i>A. mellifera</i>	0.3284	0.0909	3.614	<0.001***
		Butterflies	−0.2305	0.1126	−2.047	0.04*
		Bumble bees	0.2756	0.003	91.75	<0.001***
Isolation of less-intensively managed and semi-natural patches	APP					
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
		<i>A. mellifera</i>	−0.2341	0.094	−2.491	0.01*
		Hover flies	−0.2505	0.0026	−96.536	<0.001***
Daily temperature (°C)	OSR	All groups	0.2197	0.0784	2.802	0.005**
		<i>A. mellifera</i>	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 (°C)	APP	Bumble bees	−0.3429	0.003	−114.10	<0.001***
		Solitary bees	0.3331	0.0021	156.6	<0.001***
		All groups	0.2734	0.0808	3.384	<0.001***
		Bumble bees	−0.5060	0.1109	−4.562	<0.001***
	OSR	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*

(Continued)

TABLE 1 (Continued)

Variable	Crop	Insect group	Estimate	Standard error	Z-Value	p-value >Z
Annual precipitation	APP	All groups	0.12057	0.06986	1.726	0.08
		<i>A. mellifera</i>	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**
Precipitation seasonality	APP	Butterflies	−0.5528	0.1257	−4.396	<0.001***
		<i>A. mellifera</i>	0.5088	0.124	4.104	<0.001***
		Bumble bees	−0.2362	0.003	−78.64	<0.001***
	OSR	Butterflies	0.8481	0.1454	5.832	<0.001***
		Bumble bees	−0.2387	0.1047	−2.279	0.02*
Annual temperature (°C) * landscape diversity (SHDI)	OSR	Solitary bees	0.4247	0.1345	3.157	0.002**


The significant codes are: 0 <***<0.001 <*<0.01 <*<0.05 <.<0.1.

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 floral resources and high flower density (Hoyle et al., 2007; Rollin et al., 2013; Vrdoljak et al., 2016; Woodcock et al., 2016; Magrach et al., 2017; Van Reeth et al., 2018). 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 and Raine, 2022), some fungicides can negatively impact the behavior and fitness of honey bees [European Commission Implementing Regulation EU, 2018, (2018/1865 of 28 November 2018); Liao et al., 2019]. Moreover, some pollinator groups might have been attracted to the target crops by other species of plant growing within and along the margins of the fields, despite the pollen and nectar resources offered by the target crops during sampling. The composition and abundance of these non-crop plants may also differ between sites, as a result of fundamental differences in cultivation between our two focal crops; oilseed rape being 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 center 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 Brassiceae), 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.

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 (Rundlöf et al., 2008b; Marini et al., 2012b; Nayak et al., 2015; Raderschall et al., 2021; Martínez-Núñez et al., 2022). 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 (Cane and Sipes, 2007; Eckhardt et al., 2014; Bertrand et al., 2019), and during different stages of their life cycle (Erhardt, 1985; Erhardt and 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 (Timberlake et al., 2019; Bottero et al., 2021). 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

TABLE 2 Summary of the positive (“+”) and negative (“–”) effects of landscape and climate variables on the abundance of the six groups of pollinators.

		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 bee	–									+	+	
	Syrphids		–		+								
	Butterflies					–			+				
	All taxa			+						+	+	–	
	Honey bees					–			+	+			
	Bumble bees			+							–		–
	Solitary bee				+					+	+	–	
	Syrphids					–					+		
	Butterflies			+					–	+	+	–	

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 (value of $p < 0.05$; in black) and those representing a trend ($0.05 < \text{value of } p < 0.1$; in grey) are shown in the table.

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.

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 and Initiative, 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 honey bees and bumble bees, which are known for their long foraging distances (Beekman and Ratnieks, 2000; Knight et al., 2005; Carvell et al., 2012). 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 (Stanley and Stout, 2013; Riedinger et al., 2015; Holzschuh et al., 2016; Grab et al., 2017; Bänisch et al., 2021; Osterman et al., 2021). 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.

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 presence of mass-flowering crops and orchards in the adjacent patches and the abundance of both honey bees and hover flies at the focal site. The proximity of competing mass-flowering crops and orchards in the vicinity of a site 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 and Mevi-Schütz, 2009), and thus can strongly benefit from the presence of semi-natural habitats that offer a greater diversity of floral and nesting resources (Steffan-Dewenter et al., 2002; Rundlöf et al., 2008a, 2008b; Nayak et al., 2015). 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 and Stout, 2013).

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 behavior 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 managed by beekeepers, especially since many other orchards were found in the vicinity, and may have influenced the abundance of other insect groups. 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 behavior, mating opportunities and oviposition resources at the patch and landscape level (Dover and Settele, 2009). 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.

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.

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, 2010–2014). 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 (Tepedino and Parker, 1986; Weidenmüller et al., 2002; Radmacher and Strohm, 2010; O'Neill et al., 2011; Holland and Bourke, 2015; Miller-Struttmann et al., 2015; Gerard et al., 2018a,b; Martinet et al., 2021). 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 and 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).

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 and 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 and Rands, 2019). Although both apple and oilseed rape flowers are characterized 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 and 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 (Pyke and Waser, 1981; Baker and Baker, 1983; Lawson and Rands, 2019), 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.

Conclusion

The adoption of a standardized insect sampling protocol across 128 structurally different sites characterized 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, characterized 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 and Sparks, 2000; Marshall and Moonen, 2002; Cranmer et al., 2012).

Broadly, our take-home message is that despite some taxonomic variation, landscape simplification negatively affects some important pollinating insect taxa. In addition, our results show a negative impact of high temperature on bumble bee abundance. Taken with other studies, which have reported similar findings for other taxonomic groups, there may be widespread implications of landscape simplification and climate change on multifunctionality and the delivery of multiple ecosystem services (Mooney et al., 2009; 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 characterized 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.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

MA, MB, PR, CD, SH, KI, A-MK, MM, VM-L, SP, MR, OS, and JSt: study design. MB, PR, A-MK, MM, OS, CC, JM, MA, MR, SP, and JSt: funding and resources. MA, EA, IB, MB, CC, PR, JM, GP, SH, AK, VM-L, SP, PM, RR, MR, OS, and JSt: protocol development. MA, IB, EC, CC, PR, GP, CD, DDU, SH, A-MK, AK, VM-L, PM, HP-P, MR, JSc, OS, DS, GT, and ET: data collection. IB, CD, OS, and JSt: analysis and interpretation of results. IB, CD, and JSt: draft manuscript preparation. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1128228/full#supplementary-material>

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