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Effects of agricultural landscape heterogeneity on pollinator visitation rates in Mediterranean oilseed rape

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ABSTRACT

Agricultural intensification, by changing land use and modifying the yearly configuration and composition through crop sequences, affects the abundance and diversity of pollinators and, consequently, pollination. This study aims to assess the impact of the characteristics of agricultural landscapes on pollinator abundance in the Mediterranean region. We studied the response of three major wild pollinator groups (hoverflies, bumblebees, and wild bees) to four landscape characteristics: three related to composition, namely, equivalent crop diversity in the sampling year (eRg), previous year equivalent crop diversity (eRgP) and percentage of seminatural habitats (SNH), and one related to landscape configuration, namely, mean field size (MFS). For this evaluation, we selected twenty-two oilseed rape fields (OSRs) differing in surrounding landscape characteristics within a 1-km radius. Multimodel inference indicates that landscape variables affect pollinator groups differently. The percentage of SNH was the most important variable having a positive influence on the abundance of bumblebees, while eRgP and MFS were found to be important for the abundance of wild bees and hoverflies. These data allow us to prioritize actions aimed at specific groups of pollinators, improve agricultural landscape schemes, promote the conservation of wild pollinators, promote crop diversity at the landscape scale and increase the extent of seminatural areas.

1. Introduction

Pollinators provide essential services for the sexual reproduction of many wild plant species and increase the yields of many globally traded food and biofuel crops (Bommarco et al., 2012; Klein et al., 2007; Raderschall et al., 2021). It is estimated that one-third of food depends, directly or indirectly, on entomophilous pollination, an amount that represents approximately 153 billion € per year worldwide (Gallai et al., 2009). Therefore, maintaining sufficient levels of pollinators in the landscape is key to preserving plant diversity and ensuring food production (Balzan et al., 2014; Dainese et al., 2019).

In the last 50 years, a marked decrease in the abundance of bees has been observed (Biesmeijer et al., 2006; Zattara and Aizen, 2021), so pollination is considered a declining ecosystem service (Kearns et al., 1998; Klein et al., 2007). The decline in pollinators has been attributed to diverse anthropogenic causes, such as land use changes caused by the intensification of agricultural land management (Hass et al., 2018; Kennedy et al., 2013; Kovács-Hostyánszki et al. 2017; Raven and Wagner, 2021). Agricultural intensification has modified the configuration and composition of agricultural landscapes through the reduction and fragmentation of seminatural habitats (SNH), the enlargement of fields and the reduction of crop diversity, which has homogenized agricultural land (Gámez-Virués et al., 2015; Tilman et al., 2001). All these factors have altered the functioning of agroecosystems, generating loss of feeding and nesting opportunities and resulting in a decrease in pollinator populations such as wild bees (Wersebeckmann et al., 2023).

The maintenance of pollinators and pollination services requires the availability of sufficient resources in both noncultivated areas and crops of these agricultural landscapes (Ricketts et al., 2008). These resources include suitable nesting habitats as well as sufficient nectar- and pollen-rich floral resources within their flight ranges (Le Feon et al., 2010; Liczner and Colla, 2019). While floral resources can be obtained both in noncrop and crop areas, many pollinators cannot complete their life cycle in crops but visit them only to forage, and their nesting habitats

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are usually found in noncrop areas (Cavigliasso et al., 2022; Williams and Kremen, 2007).

To supply the resources and habitats needed by pollinators, agricultural landscapes need to display a certain degree of heterogeneity, which relates to two different components, configuration and composition. Mean field size is a characteristic related to landscape configuration, as it determines field boundary density and the availability of small linear noncropped fragments, increasing connectivity with natural and seminatural areas (Hass et al., 2018). On the other hand, both noncrop areas and cropped areas contribute to the compositional heterogeneity of agricultural landscapes. Several authors have shown that the extent of seminatural habitats (SNH) has a positive relationship with the abundance and diversity of wild bee communities (Bukovinszky et al., 2017; Loyola and Martins, 2008; Nayak et al., 2015; Rollin et al., 2013). Moreover, landscapes with larger extents of seminatural habitats and higher connectivity have also been shown to increase yields in different crops through pollinators and their pollination services (Castle et al., 2019; Martin et al., 2019; Petersen and Nault, 2014; Rollin et al., 2013). However, the proportion of SNH present in agricultural landscapes may not provide sufficient pollen and nectar resources to maintain viable pollinator populations. Therefore, the relationship between SNH and pollinators can be strongly affected by the floral resources offered by crops in agricultural landscapes (Bartual et al., 2019; Holzschuh et al., 2011; Winfree et al., 2007). Agricultural landscape composition can also vary in relation to the crop diversity in a landscape. Crop diversity has been reported to have a positive relationship with the abundance of pollinators by providing a more diverse matrix of food resources and habitats for nesting and dispersal (Fahrig et al., 2011; Raderschall et al., 2021; Sirami et al., 2019). Especially in cereal-dominated arable land, the diversity of crops, some of which have abundant floral resources, allows pollinators to complement their diet (Fahrig et al., 2011).

Mass-flowering crops offer abundant floral resources and are very attractive to a wide diversity of pollinators (Holzschuh et al., 2011). At a low proportion, these crops have a concentration effect in agricultural landscapes, they can be used as phytometers to obtain estimates of the abundance of pollinators in the landscape during flowering (Magrach et al., 2018; Martínez-Núñez et al. 2022). Oilseed rape (*Brassica napus* L.) (OSR) is a mass-flowering crop that is widely cultivated worldwide and can concentrate the abundance of pollinators in the agricultural landscape(Beyer et al., 2021; Mendoza-García et al., 2018). Wild pollinators that visit oilseed rape flowers include honeybees, wild bees, bumblebees, hoverflies and flower-visiting beetles (Rader et al., 2009; Stanley et al., 2013).

However, the composition of the agricultural landscape varies from year to year, especially in arable landscapes, where the crops grown are mainly annuals. Thus, a deeper knowledge about pollinators and their interactions with landscape elements, as well as with crop diversity and its temporal changes, could help in promoting the pollinator community and its pollination services.

In recent years, some progress has been made in understanding the effect of changing heterogeneity at the agricultural landscape level on the abundance and diversity of pollinators. However, the abundance of pollinators increases with increasing availability of resources, the role of the spatiotemporal compositional heterogeneity of the landscape on the different pollinator groups is still unknown, especially in Mediterranean agricultural landscapes.

We studied the response of three major wild pollinator groups (hoverflies, bumblebees, and other wild bees) to four landscape characteristics related to the configurational and compositional heterogeneity of agricultural landscapes. We selected 22 OSR fields in Mediterranean agricultural landscapes of Spain, and we tested the following hypotheses: (1) landscape metrics related to cropland (i.e., crop diversity and mean field size) and seminatural habitats in agricultural landscapes have a differential effect on the abundance of different group of pollinators, and (2) Temporal changes in crop diversity influence the abundance of pollinators that visit OSR fields.

2. Materials and methods

The study was conducted in the spring of 2021 and 2022 in central Catalonia in northeastern Spain (Fig. 1). The landscape is dominated by rainfed arable crops, mainly winter cereals such as wheat, barley or spelt interspersed with woody crops common to the Mediterranean region, such as olive groves and vineyards but many others such as alfalfa, fruit trees, chickpeas, lentils, almond, onion, pumpkin, corn or oilseed rape (Institut d'Estadística de Catalunya 2023). The noncropped areas are mainly occupied by various types of forest habitats (pine forests, holm oak forests, oak groves), shrubs derived from their degradation (usually by fire) or bushes and mesoxerophilic grasslands that occupy former crops and other marginal areas (Departament de Territori i Sostenibilitat, 2018).

2.1. Landscape metrics

We selected conventionally managed OSR fields, all sown to hybrid winter OSR varieties, with varieties differing between farmers. For the characterization of the landscape, we selected a circular area of 1 km radius around each OSR field. The radius was chosen because previous studies have shown that most foraging flights for wild bees are within this distance and corresponds to the range of the average landscape response for hoverflies (Holzschuh et al., 2011; Madureira et al., 2023; Steffan-Dewenter and Kuhn, 2003). We selected 22 localities in which the area sown with OSR around the selected fields was less than 10% to ensure the concentrating effect on bees (Beyer et al., 2021; Magrach et al., 2018). All localities were at least 2 km apart to prevent any two OSR fields from being visited by the same pool of pollinators (Holzschuh et al., 2016; Westphal et al., 2003).

The characterization of the composition and configuration of the landscape around each of the OSR fields was carried out based on the spatial information of the DUN-SIGPAC Crop Map (Departament d'Acció Climàtica, Alimentació i Agenda Rural 2023) and the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018) using R software with package sf (Edzer Pebesma, 2018). Four landscape metrics were calculated for each circular area. Three of them are related to composition: the equivalent crop group diversity (eRg) for the current year, the equivalent crop group diversity for the previous year (eRgP) and percentage of area occupied by seminatural habitats. To compute the latter, crop groups were defined according to their functional contribution to pollinators, e.g., wheat, barley, oats, and spelt are included in cereal functional groups (see all groups in Table A.1). With these functional groups, the eRg metric was obtained by calculating the Shannon index (Eq. 1), weighting the groups according to their proportion of the landscape area (p_i), and converting it into true diversity (Eq. 2) (Jost, 2006).

$$Hg = \left(-\sum_{i=1}^{s} p_i \ln p_i\right) \tag{1}$$

$$eRg = \exp(Hg) \tag{2}$$

The equivalent crop group diversity corresponds to the effective number of crop functional groups if all crop groups were equally represented. We also computed the equivalent crop group diversity of the previous year with the same method but using crop data for the preceding year. The fourth metric is related to configuration, and we used the mean field size (MFS). A detailed listing of the characteristics of the studied agricultural landscapes is provided in Table A.3.

2.2. Pollinator evaluation

Sampling was carried out in each OSR field during April and May

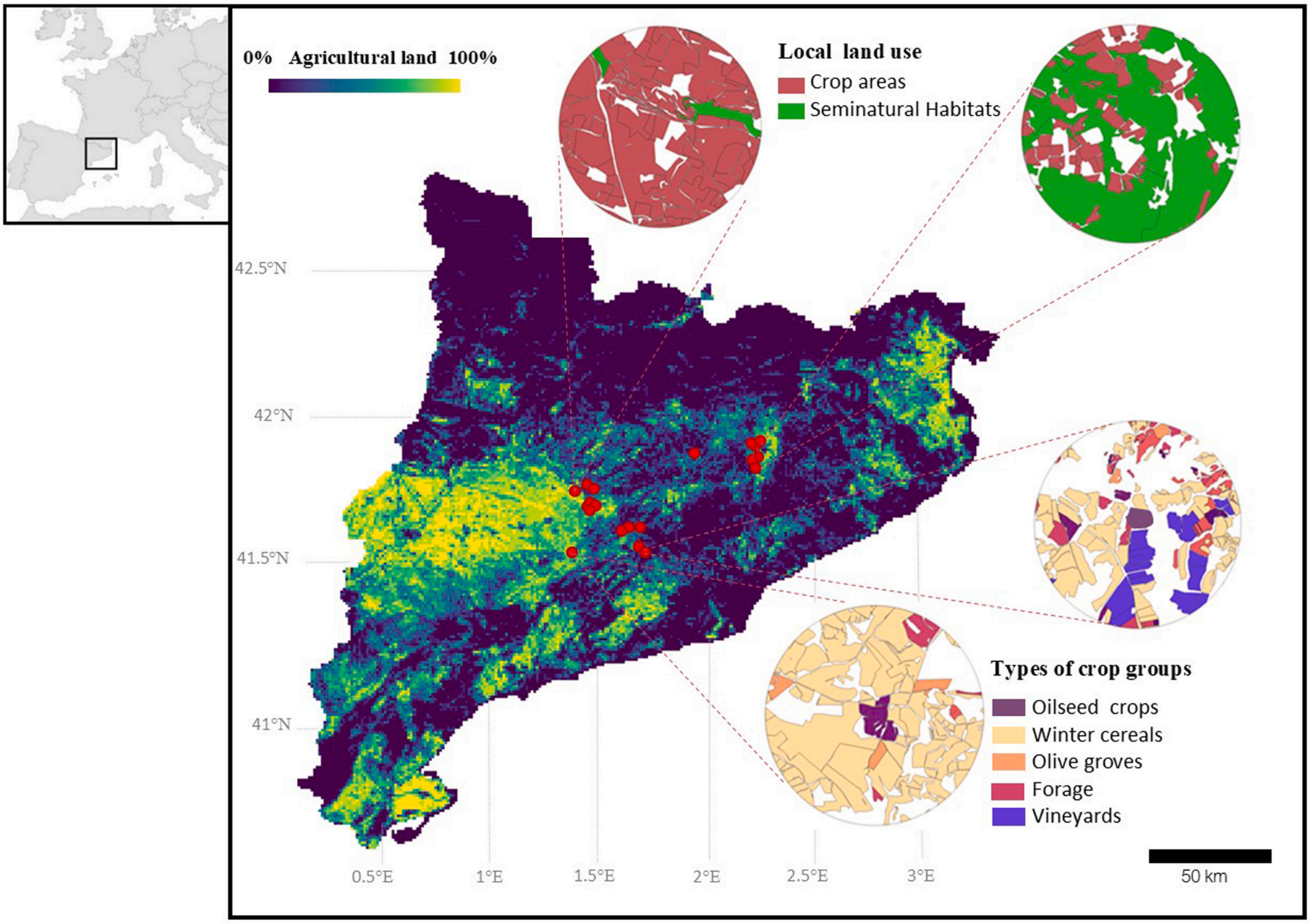

Fig. 1. Map of Catalonia (NE of Spain) and the distribution of the 22 localities. The blue—yellow gradient represents the percentage of agricultural land. Information available in the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018). The circles represent the agricultural landscape around the localities, and this buffer zone has a radius of 1 km. The upper circles represent examples of landscapes with contrasting local land use. The lower circles represent examples of landscapes with contrasting diversity of crop groups. Only five of the thirteen types of crops present in the 22 agricultural landscapes are shown, complete list in Table A.1.

(2020 or 2021 depending on the field). We only evaluated the abundance of insects that have been classified as efficient wild pollinators (Jauker et al., 2009). We recorded three groups: wild bees, bumblebees, and hoverflies. The abundance of the honeybee (*Apis mellifera* L. 1758) was also recorded since it could affect the behaviour of the rest of the wild pollinators (Hudewenz and Klein, 2013), although it was not analysed since it depends more on farmers' preferences than on landscape properties.

One observer recorded insects visiting OSR flowers on two different days during peak flowering in two transects of 150 m^2 each (75 × 2 m) parallel to the field margin, one at the crop edge and the other in the field centre (25 m away from any field margin). We sampled on these positions within the crop to estimate the effect of the distance to margins in the floral visitors. The abundance of each group of pollinators was calculated by adding the observations of the two sampling days together for the field centre and the edge separately. The total sampling effort was 15 minutes/transect/day × 2 transects/field × 2 days = 60 minutes/field.

2.3. Data analysis

The analysis of the relationship of the abundance of the pollinator groups and total abundance of pollinators with landscape variables was carried out using generalized linear mixed models using the 'glmmTMB' package (Brooks et al., 2017). We used the variance inflation factor (VIF) to test for potential collinearity between explanatory variables (Zuur et al., 2010), but the VIF was below 4 in all cases (Table A.2). The relationship between landscape variables and the abundance of pollinators was tested. As fixed effects variables, we included eRg, eRgP, MFS and SNH as continuous variables (scaled to minimum = 0 and maximum = 1) and within-field position (edge and centre) and year as categorical variables. Locality was included as a random effect factor since the abundance of pollinators between localities was variable.

We ran all possible model combinations using the 'dredge' function in the 'MuMIn' package (Barton and Barton, 2023) to test several hypotheses simultaneously across the models. For each pollinator group, we explored the set of 64 models that included all possible combinations of the four landscape variables plus within-field position and year, and a null model. For each model, we computed its Akaike information criterion corrected for small sample sizes (AICc). We averaged the whole set of models (Burnham, 2002). For each average model, the 90% and 95% confidence intervals of coefficients and their weights (w_i) were obtained. We report all predictor variables (Σw_i). All analyses were performed in the R environment v3.4.4 (R R Core Team, 2020).

3. Results

During the study, 1462 pollinating organisms were recorded contacting the OSR flowers, of which 16.3% corresponded to the group of hoverflies, 18.9% to bumblebees and 65.5% to wild solitary bees.

Within-field position and crop diversity from the previous year (eRgP) at the agricultural landscape have a positive and significant impact on the abundance of total pollinators visiting OSR fields. The average model indicates strong support for each of these variables, according to their accumulated weights (Σw_i, 0.79 and 0.69, respectively) and their CI (Table 1) (Fig. 2). The other metrics studied (SNH, MFS, and eRg) had less clear effects with lower weights and their CI including zero.

3.1. Response of bumblebees to landscape metrics

The seminatural habitats and mean field size in the landscape have an impact on bumblebee abundance visiting OSR fields. The average model has substantial support, both in terms of relative importance and CIs (Table 1). The landscape variables SNH ($\Sigma w_i = 0.95$) and MFS ($\Sigma wi = 0.71$) both had a positive effect on bumblebees (Fig. 3), and the variable eRgP ($\Sigma wi = 0.37$) also had a positive effect; however, the confidence interval of the latter contained zero. On the other hand, eRg ($\Sigma wi = 0.27$) and within-field position ($\Sigma wi = 0.24$) (Fig. 2) were not significant.

3.2. Response of wild bees to landscape metrics

The abundance of wild bees that visit OSR responds to three of the agricultural landscape variables that were examined: eRgP, MFS in crop areas and the amount of SNH that is present in the noncropped areas. The average model has eRgP ($\Sigma wi = 0.65$) as the most important variable, which has a positive effect on this group of pollinators (Fig. 3). Additionally, SNH ($\Sigma wi = 0.62$) and MFS ($\Sigma wi = 0.47$) have a high relative weight, both of which have a negative effect, although the interval of MFS includes 0 at 90% CI (Table 1). Thus, there is strong support for the influence of these three factors on wild bees. Different patterns occur with eRg ($\Sigma wi = 0.34$) and within-field position ($\Sigma wi = 0.30$) (Fig. 2), which have lower weights.

3.3. Response of hoverflies to landscape metrics

The effect of within-field position (edge) ($\Sigma wi = 0.93$) was significant for the hoverflies, supported by their CI (Table 1) (Fig. 2). Two of the remaining agricultural landscape variables, MFS ($\Sigma wi = 0.56$) and SNH ($\Sigma wi = 0.56$), both had a clear negative effect (Fig. 2), although the confidence intervals of these variables included zero. The remaining models included the other agricultural landscape variables, eRgP and eRg, but with lower weights $\Sigma wi = 0.30$ and $\Sigma wi = 0.28$, respectively (Table 1).

4. Discussion

Our study reveals that pollinator abundance responds to within-field position and past year crop diversity, moreover, the responses to seminatural habitat cover, mean field size and past and current crop diversity differed between the pollinator groups assessed.

These findings support our first hypothesis: Each group of pollinators reacts differently to landscape features. The proportion of seminatural areas and mean field size have a strong positive effect on the abundance of bumblebees and a negative effect on other wild bees. Wild bees respond positively to past crop diversity. Hoverflies, on the other hand, respond to field environment rather than to landscape features.

Our second hypothesis has been partially supported. Past crop diversity has a consistently positive effect across all three pollinator groups, although its strength is variable. This effect is particularly strong (statistically significant) for wild bees, which are the most abundant group of pollinators in our study.

4.1. Past and present effects of crop diversity

Crop diversity in the current year had no significant effect on the abundance of any pollinator group. Although increasing last year's crop diversity correlated positively with the abundance of all three pollinator

Table 1
Estimates and standard error (SE) for each predictor in the average models obtained through multimodel inference. For each fixed effect factor, its confidence intervals (CI at 90% and 95%) and sum of weights (Σw_i) are indicated. Bold numbers indicate cases where the confidence intervals do not include 0. eRg: Crop Diversity, eRgP: Previous Year Crop Diversity, MFS: Mean Field Size, SNH: Seminatural Habitats percentage.

		Estimate	SE	Σwi	CI			
					-2.50%	**-5%**	**-95%**	**-97.50%**
a) Total Pollinators								
	Year (2022)	8.955	3.299	0.9	**2.489**	**3.547**	**14.364**	**15.422**
	Edge	3.659	1.633	0.79	**0.457**	**0.981**	**6.336**	**6.86**
	eRgP	4.473	2.136	0.69	**0.286**	**0.971**	**7.976**	**8.661**
	SNH	-1.672	1.995	0.32	-5.583	-4.944	1.6	2.238
	MFS	-2.825	2.827	0.38	-8.366	-7.464	1.814	2.715
	eRg	1.174	2.648	0.29	-4.016	-3.17	5.519	6.364
b) Bumblebees								
	SNH	2.689	0.909	0.95	**0.907**	**1.197**	**4.181**	**4.472**
	MFS	2.22	1.204	0.71	-0.139	**0.244**	**4.196**	4.58
	eRgP	0.999	1.298	0.37	-1.546	-1.132	3.13	3.544
	Year (2022)	-1.438	1.503	0.34	-4.385	-3.903	1.026	1.508
	eRg	0.169	1.07	0.27	-1.928	-1.586	1.924	2.266
	Edge	0.09	0.553	0.24	-0.994	-0.816	0.998	1.175
c) Wild Bees								
	Year (2022)	7.725	2.442	0.96	**2.938**	**3.721**	**11.729**	**12.511**
	eRgP	3.299	1.662	0.65	**0.04**	**0.572**	**6.026**	**6.558**
	SNH	-2.529	1.428	0.62	-5.328	**-4.871**	**-0.186**	0.269
	MFS	-2.867	2.213	0.47	-7.206	-6.501	0.766	0.195
	eRg	1.645	1.83	0.34	-1.943	-1.358	4.648	5.233
	Edge	0.727	0.913	0.3	-1.062	-0.769	2.223	2.517
d) Hoverflies								
	Edge	2.84	1.013	0.93	**0.854**	**1.179**	**4.502**	**4.827**
	MFS	-2.227	1.422	0.56	-5.06	-4.561	0.106	0.56
	SNH	-1.894	1.161	0.56	-4.17	-3.799	0.009	0.381
	Year (2022)	3.028	1.91	0.52	-0.716	-0.104	6.161	6.774
	eRg	-0.472	1.38	0.28	-3.178	-2.737	1.792	2.234
	eRgP	0.654	1.504	0.3	-2.293	-1.813	3.123	3.603

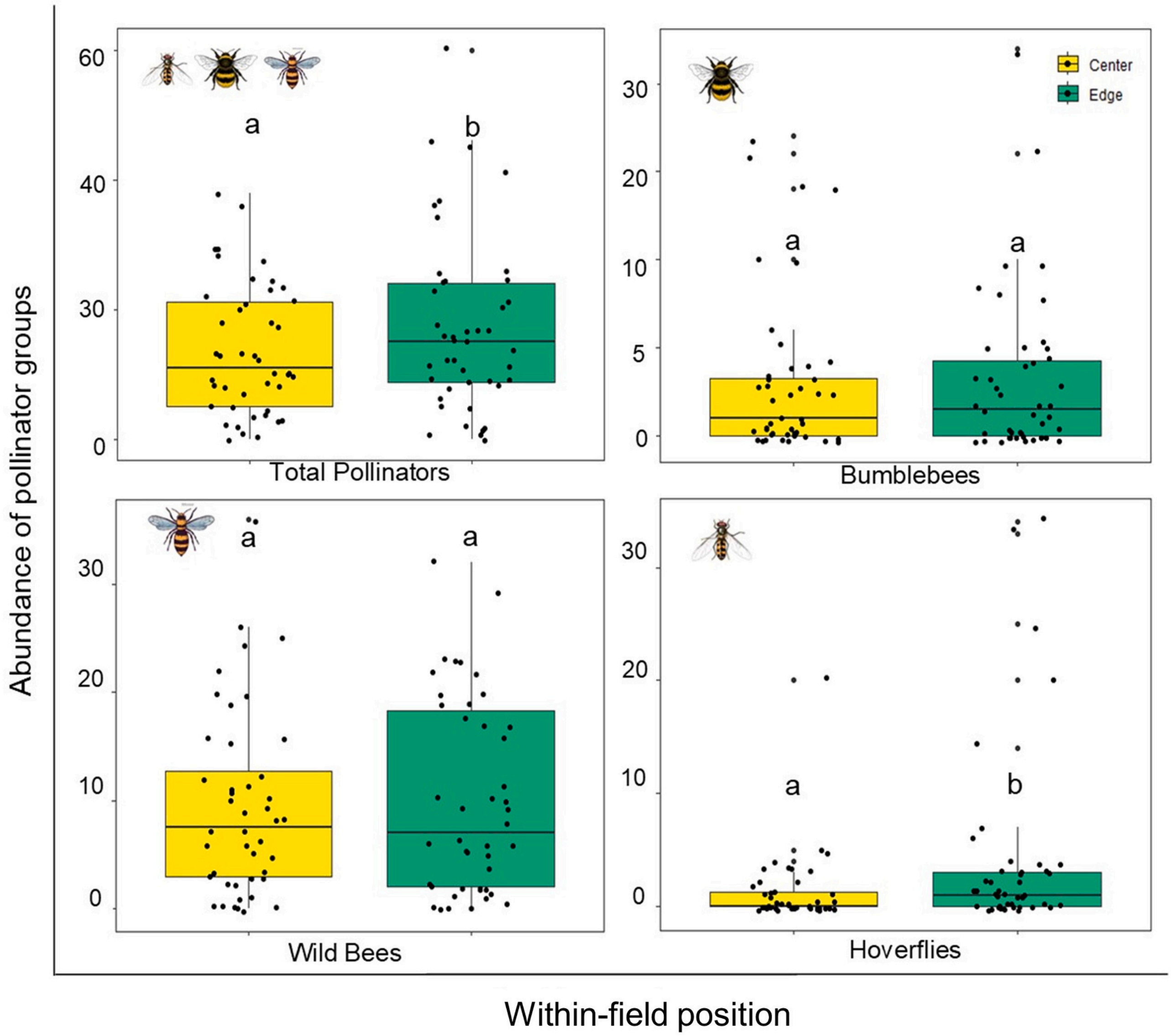

Fig. 2. Effects of within-field position on the abundances per field of total pollinators and the three pollinator (hoverflies, bumblebee and other wild bee) groups studied. Model predictions with 95% confidence intervals were obtained from the average model of the multimodel analysis (Table 1). Different letters above boxes indicate significant differences between within-field position, centre (yellow) and edge (green).

groups, statistical significance was observed solely in the case of wild bees and when considering the collective abundance of all three pollinator groups. The abundance of wild bees is more related to preceding features of the agricultural landscape, with the crop diversity of the prior year of sampling being more important than the crop diversity around the area where they are thriving. This pattern is in line with earlier studies that have demonstrated how an increase in crop diversification benefits the agricultural landscape biodiversity of wild bees (Martin et al., 2019; Sirami et al., 2019) and that interannual changes in crop composition are also well known to affect ecological processes such as pollination and biological control (Holzschuh et al., 2011; Schellhorn et al., 2015; Tscharntke et al., 2021). Crop diversity did not affect bumblebee abundance, in clear contrast with earlier studies, which indicated that high crop diversity was related to higher bumblebee prevalence in the agricultural landscape (Hemberger et al., 2021). For hoverflies, our findings are consistent with those of Hass et al. (2018) in that they also show that the abundance of these insects is independent of crop diversity.

According to recent studies, crop diversification in highly intensified landscapes creates spatial and temporal heterogeneity of habitats and resources that enable bee populations to be sustained at higher levels (Beyer et al., 2021; Cavigliasso et al., 2022). This may hold a relationship with our findings, where past year crop diversity had a stronger effect on the abundance of pollinators than crop diversity in the current year. Similar effects have been observed in relation to the presence of mass flowering crops, as they can contribute to pollinator population growth, and spillage is generated to plants in noncultivated areas as well as to other crops (Blaauw and Isaacs, 2014). Therefore, planning agricultural schemes that increase crop diversity and consider crops producing flower resources could be relevant in relation to the maintenance of pollinators or the provision of pollination services in the following year.

4.2. Relationship between seminatural areas and pollinators

Our findings suggest that the proportion of seminatural areas in the landscape is important for the abundance of the three pollinator groups, even though they exhibited the contrasting pattern. While solitary bees and hoverflies benefit from lower percentages of seminatural habitats, bumblebees were more abundant when the landscape had a higher

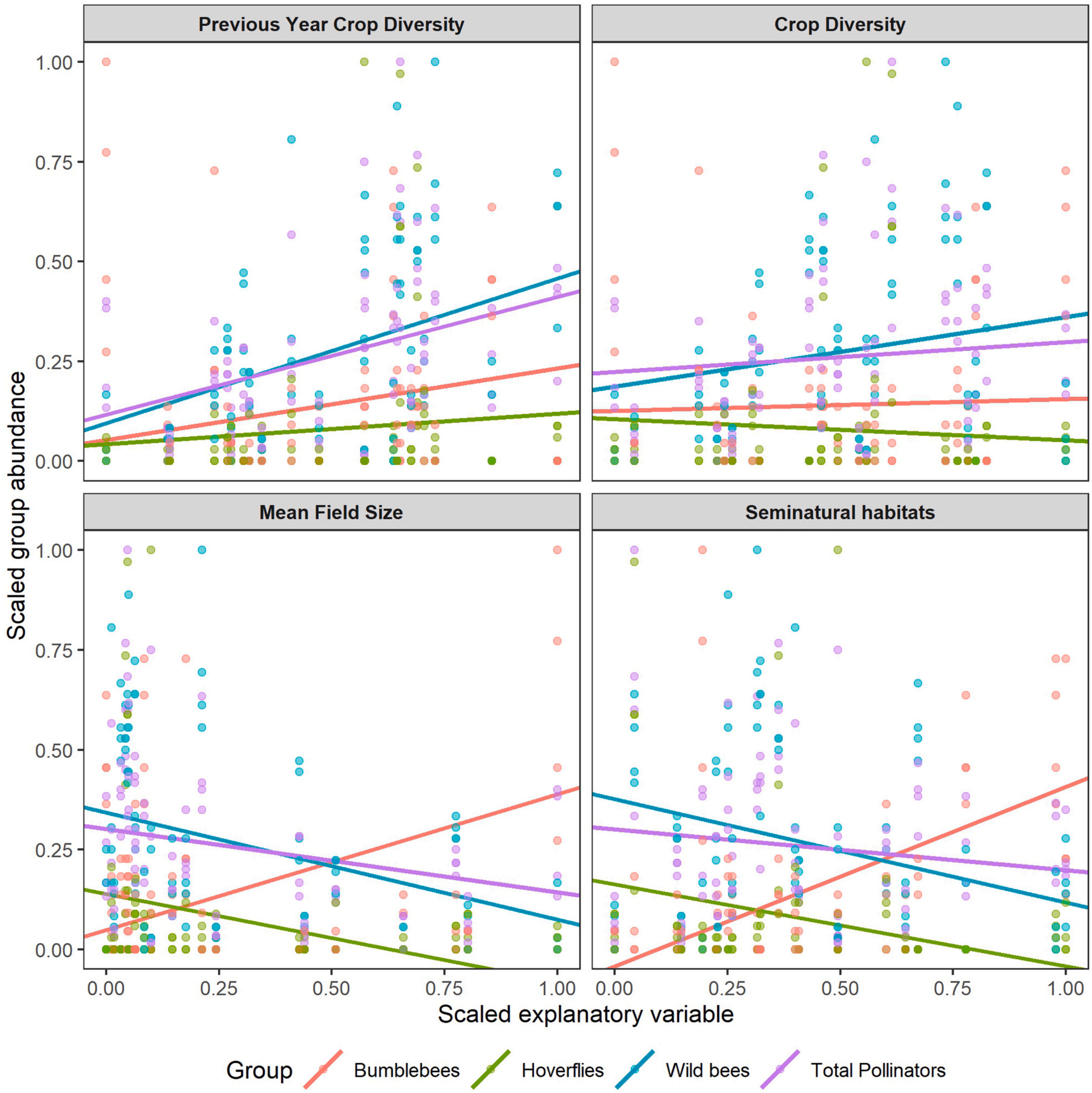

Fig. 3. Effect of landscape variables on the abundances of the three pollinator groups studied and the total pollinators. Lines represent the model predictions for each metric of the agricultural landscape and were obtained from the average model of the multimodel analysis.

proportion of these habitats.

Wild bees have a more restricted flight range than other pollinators. Hofmann et al. (2020) recommended that wildflower strips be available within a radius of 150 m to maximize the effect on wild bees. Although wild bees benefit from soil and wooden structures, they can use isolated trees in less dense or disturbed areas and anthropic areas, such as cultivated areas, to establish their nests or colonies (Bosch and Kemp, 2002; Hellwig et al., 2022; Rollin et al., 2013). Due to this spatial scale of their habitats and their range of resource utilization (500 m) (Tscharntke et al., 2005), it is possible that seminatural habitats negatively affect the abundance of wild bees in nearby flowering fields. A negative relationship between wild bees and seminatural habitats has already been reported in the Mediterranean region, and it is possible that seminatural forested areas, such as those that predominate in the study area, act as barriers that isolate the fields (Carré et al., 2009; Fagan et al., 1999; Morrison et al., 2017).

Aligned with our findings, Cavigliasso et al. (2022) observed a decline in solitary bee abundance with an increased forest proportion, while Martin et al. (2019) highlighted the significance of landscape edge density for the thriving of solitary bees rather than seminatural areas. Consequently, it appears that not all natural habitats equally benefit wild bees; for instance, forested areas may not favor solitary bees as much as habitats within field margins do. These margins, hosting grassland and thicket remnants, demonstrate greater benefits as supported by studies such as Maurer et al. (2022), Westphal et al. (2003) emphasizing the importance of increased field margin density.

The negative trend between hoverflies and seminatural areas in our study is similar to those obtained in other investigations that report that their abundance even increases in cultivated areas when the seminatural areas are further away from them (Hass et al., 2018; Jauker et al., 2009; Schirmel et al., 2018). This may be because their movement and the availability of (larval) food sources (aphids for some hoverfly species) are enhanced by cultivated areas, especially for generalist species, which are generally found in agricultural landscapes (Haenke et al., 2014; Jauker et al., 2009; Speight, 2017).

On the other hand, for bumblebees, the proportion of seminatural areas had a positive effect and was the most important variable explaining their abundance. This positive relationship between bumblebees and the proportion of seminatural areas agrees with previous research (Hopfenmüller et al., 2014; Raderschall et al., 2021). Bumblebees prefer environments that have constant resources, such as those offered by natural and seminatural habitats. Furthermore, bumblebee habitat is enhanced by heterogeneous landscapes comprising a variety of seminatural habitats (Proesmans et al., 2019), and certain species of the genus *Bombus* use uncropped areas to form colonies (Goulson et al., 2008; Kells and Goulson, 2003).

4.3. Agricultural landscape configuration and its relationship with pollinators

The mean field size has a positive correlation with the abundance of bumblebees visiting OSR. Bumblebees are more abundant in environments with larger fields and thus fewer crop margins. Bumblebees have larger body sizes, which allows them to have larger foraging ranges and makes them less reliant on herbaceous habitats in intensive agricultural landscapes (Gathmann and Tscharntke, 2002; Westphal et al., 2006). Bumblebees feed instead on available natural resources present in seminatural woody areas but can exploit mass-flowering crops when present in the landscape (Rollin et al., 2013). This is the case with *Bombus terrestris* L. 1758, a species that can adapt readily due to its generalist behaviour (Dafni et al., 2010).

Conversely, field size has been proposed as a reliable and widely available indicator that can help identify potential areas of high natural value since reducing field size can bring substantial benefits to biodiversity (Clough et al., 2020). Previous research has reported a 70% higher abundance of pollinators on small fields (Martin et al., 2019). Smaller fields with more margins facilitate pollinator movement by boosting landscape connectivity (Hass et al., 2018; Magrach et al., 2023; Sutherland et al., 2001). Benefits of field size could be enhanced by the negative correlation that exists with crop diversity ($p < 0.05$). According to other studies, wild pollinators such as solitary bees nest mainly outside of arable fields (Clough et al., 2020). Therefore, field margins not only increase connectivity but also contribute to the stabilization of pollinator populations (Gardner et al., 2021; Mendoza-García et al., 2018). The relationship of field size with hoverflies is not straightforward. Some studies have shown that the presence of margins in cultivated fields benefits hoverflies because it provides habitat and floral supplies (Schirmel et al., 2018; Sutherland et al., 2001). In our case, we found a field-level response to the proximity of the field margin, related to the greater abundance of hoverflies on the edge compared to the centre of the crop, but no landscape-scale effects of field size. Similar to data from Hass et al. (2018), who also found where hoverflies do not respond to the average field size or crop diversity.

4.4. Conclusions

The results of our study may have a few significant implications for pollinator conservation in Mediterranean climate agricultural landscapes to report how different groups of pollinators respond differently to landscape properties. This feature indicates that it is important to define a target group of pollinators for the trade-offs that are considered in agricultural landscape planning.

Despite the difficulty of changing the configuration of an agricultural landscape, composition is a more controllable landscape quality. The crop diversity would be the easiest target landscape feature for benefiting pollination services. Adjusting crop diversity can have a faster influence on pollination due to the inherent dynamic nature of crops in arable landscapes and its positive effect on wild bees, which are the most abundant group of pollinators.

On the other hand, promoting the maintenance of seminatural habitats, although less amenable to management, can have an impact on bumblebee conservation. A balance between the persistence of natural habitats, mean field size, and increasing crop diversity can benefit the populations of different guilds of pollinators and thus their pollination service in agroecosystems.

Landscape-scale management of crop planning both spatially (crop diversity and field size) and temporally were all important and can be considered complementary to seminatural habitats. The information presented in this study reinforces its value in the design of agricultural landscape schemes for pollination service preservation.

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CRediT authorship contribution statement

Sans F. Xavier: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. **Olave Magdalena:** Formal analysis, Investigation, Visualization, Writing – review & editing. **Caballero-López Berta:** Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing. **Neira Pablo:** Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Writing – review & editing. **Blanco-Moreno José Manuel:** Data curation, Methodology, Supervision, Validation, Visualization, Writing – review & editing, Conceptualization, Funding acquisition.

Declaration of Competing Interest

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Data Availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108869.

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Supplementary Information : Effects of agricultural landscape heterogeneity on pollinator visitation rates in Mediterranean oil seed rape.

Appendix A

Table A.1 List of types of crops that have been considered for the characterization of the equivalent diversity of crops (eRg).

Crop functional group	Crops
Fallows	-
Winter cereals	Khorasan wheat, common wheat, barley, oats, spelt, triticale
Summer cereal	corn, sorghum
Forage	Alfalfa, peas, barley, sainfoin, wheat, oats
Sweet fruits	Cherry trees, pear trees, apples, other fruit trees
Stone fruits	Almond, walnut, pistachio trees
Horticultural	Pumpkin, artichoke, onion, leeks, garlic, lettuce, potato, tomato
Legumes	Chickpeas, beans, lentils
Oilseeds	Oil seedrape, sunflowers
Olive groves	Olives
Other products	Herbaceous aromatics, Saffron
Proteinaceous	Peas
Vineyards	vineyards

Table A.2 VIF values for lanscape metrics

Metrics	VIF
eRg	2.454451
eRgP	3.335684
SNH	1.518418
MFS	3.617351

Table A.3 Landscape metrics characterization of the 22 studied localities

Locality	Crop Diversity (eRg)	Past Crop Diversity (eRgP)	% Semi Natural Habitat (SNH)	Mean field size (m^2) (MFS)
Cap21	4.14	3.04	0.68	12393.07
Cas21	1.65	2.08	0.03	34858.39
Cla21	3.62	3.62	0.55	9763.09
Est21	2.12	1.70	0.18	30391.48
Eula21	3.03	2.44	0.30	10123.70
Gav21	2.94	2.26	0.36	17404.58
Pil21	1.53	1.34	0.16	41075.66
Od21	3.68	4.01	0.25	11755.18
Sai21	3.57	2.60	0.46	10312.63
Sal21	2.02	1.98	0.70	15291.26
Vic21	2.72	3.14	0.20	14355.86
Al22	2.16	2.19	0.30	25680.86
Cas22	2.82	2.06	0.12	34047.72
Mor22	2.73	3.18	0.27	11111.39
Mel22	2.36	2.15	0.18	23148.39
Od22	3.44	3.29	0.24	16402.19
Spe22	3.51	3.06	0.20	11340.33
Teu22	3.13	3.08	0.06	11254.31
Ton122	2.33	3.22	0.43	11802.40
Ton222	2.65	2.87	0.48	10797.62
Ton322	2.98	2.87	0.36	12882.41

Table A.4 Set of 64 mixed generalized linear models used in the Multi-Model Inference analysis for each group of pollinators.

Model - Total Pollinators	**AICc**	**R^2 conditional**	**R^2 marginal**
year+ Within-field position + eRgP + (1 | Locality)	645.95	0.60	0.36
year+ Within-field position + eRgP + SNH + (1 | Locality)	647.94	0.60	0.37
year+ Within-field position + eRgP + MFS + (1 | Locality)	648.19	0.60	0.36
year+ Within-field position + MFS + (1 | Locality)	648.27	0.60	0.32
year+ Within-field position + eRgP + eRg + (1 | Locality)	648.31	0.60	0.36
year+ eRgP + (1 | Locality)	648.62	0.57	0.34
year+ Within-field position + MFS + SNH + (1 | Locality)	649.05	0.60	0.35
year+ Within-field position + eRg + (1 | Locality)	649.18	0.60	0.31
year+ Within-field position + eRgP + MFS + SNH + (1 | Locality)	649.68	0.60	0.38
year+ Within-field position + eRg + MFS + (1 | Locality)	650.16	0.60	0.33
year+ Within-field position + eRgP + eRg + SNH + (1 | Locality)	650.31	0.60	0.37
Within-field position + eRgP + (1 | Locality)	650.45	0.60	0.23
year+ eRgP + SNH + (1 | Locality)	650.55	0.57	0.34
year+ Within-field position + eRgP + eRg + MFS + (1 | Locality)	650.61	0.60	0.36
year+ eRgP + MFS + (1 | Locality)	650.80	0.57	0.34
year+ Within-field position + (1 | Locality)	650.86	0.60	0.23
year+ eRgP + eRg + (1 | Locality)	650.92	0.57	0.34
year+ MFS + (1 | Locality)	650.94	0.57	0.30
year+ Within-field position + eRg + MFS + SNH + (1 | Locality)	651.06	0.60	0.35
year+ Within-field position + eRg + SNH + (1 | Locality)	651.29	0.60	0.31
Within-field position + eRgP + SNH + (1 | Locality)	651.42	0.60	0.26
year+ MFS + SNH + (1 | Locality)	651.67	0.57	0.32
year+ eRg + (1 | Locality)	651.85	0.57	0.28
year+ Within-field position + eRgP + eRg + MFS + SNH + (1 | Locality)	652.17	0.60	0.38
year+ eRgP + MFS + SNH + (1 | Locality)	652.24	0.57	0.35
Within-field position + eRgP + eRg + (1 | Locality)	652.58	0.60	0.24
Within-field position + MFS + SNH + (1 | Locality)	652.66	0.60	0.24
Within-field position + eRgP + MFS + (1 | Locality)	652.74	0.60	0.23
year+ eRg + MFS + (1 | Locality)	652.77	0.57	0.31
year+ eRgP + eRg + SNH + (1 | Locality)	652.86	0.57	0.34
Within-field position + eRgP + MFS + SNH + (1 | Locality)	652.94	0.60	0.28
year+ Within-field position + SNH + (1 | Locality)	653.09	0.60	0.23
year+ eRgP + eRg + MFS + (1 | Locality)	653.17	0.57	0.34
eRgP + (1 | Locality)	653.18	0.57	0.21
year+ (1 | Locality)	653.58	0.57	0.20
year+ eRg + MFS + SNH + (1 | Locality)	653.61	0.57	0.33
Within-field position + MFS + (1 | Locality)	653.73	0.60	0.16
Within-field position + eRgP + eRg + SNH + (1 | Locality)	653.77	0.60	0.26

year+ eRg + SNH + (1 | Locality)	653.91	0.57	0.29
eRgP + SNH + (1 | Locality)	654.09	0.57	0.24
year+ eRgP + eRg + MFS + SNH + (1 | Locality)	654.66	0.57	0.35
Within-field position + eRgP + eRg + MFS + (1 | Locality)	654.87	0.60	0.24
Within-field position + eRg + MFS + SNH + (1 | Locality)	654.91	0.60	0.24
Within-field position + eRgP + eRg + MFS + SNH + (1 | Locality)	655.24	0.60	0.28
eRgP + eRg + (1 | Locality)	655.26	0.57	0.21
MFS + SNH + (1 | Locality)	655.33	0.57	0.21
eRgP + MFS + (1 | Locality)	655.41	0.57	0.21
Within-field position + eRg + (1 | Locality)	655.48	0.60	0.11
eRgP + MFS + SNH + (1 | Locality)	655.55	0.57	0.26
year+ SNH + (1 | Locality)	655.76	0.57	0.20
Within-field position + eRg + MFS + (1 | Locality)	655.91	0.60	0.16
Within-field position + (1 | Locality)	656.28	0.60	0.02
eRgP + eRg + SNH + (1 | Locality)	656.38	0.57	0.24
MFS + (1 | Locality)	656.46	0.57	0.13
Within-field position + eRg + SNH + (1 | Locality)	656.82	0.60	0.14
eRgP + eRg + MFS + (1 | Locality)	657.48	0.57	0.22
eRg + MFS + SNH + (1 | Locality)	657.53	0.57	0.21
eRgP + eRg + MFS + SNH + (1 | Locality)	657.80	0.57	0.26
eRg + (1 | Locality)	658.21	0.57	0.09
Within-field position + SNH + (1 | Locality)	658.46	0.60	0.03
eRg + MFS + (1 | Locality)	658.58	0.57	0.14
(1 | Locality)	659.06	0.57	0
eRg + SNH + (1 | Locality)	659.50	0.57	0.11
SNH + (1 | Locality)	661.19	0.57	0.00

Model - Bumblebees	**AICc**	**R^2 conditional**	**R^2 marginal**
MFS + scSNH + (1 | Locality)	465.07	0.68	0.29
eRgP + MFS + scSNH + (1 | Locality)	465.76	0.68	0.33
year + MFS + scSNH + (1 | Locality)	466.79	0.68	0.30
eRg + MFS + scSNH + (1 | Locality)	466.89	0.68	0.30
scSNH + (1 | Locality)	467.18	0.68	0.19
year + eRgP + MFS + scSNH + (1 | Locality)	467.19	0.68	0.34
Within-field position + MFS + scSNH + (1 | Locality)	467.35	0.68	0.29
year + scSNH + (1 | Locality)	467.90	0.68	0.23
Within-field position + eRgP + MFS + scSNH + (1 | Locality)	468.09	0.68	0.33
eRgP + eRg + MFS + scSNH + (1 | Locality)	468.10	0.68	0.33
eRgP + scSNH + (1 | Locality)	468.74	0.68	0.21
year + eRg + MFS + scSNH + (1 | Locality)	468.74	0.68	0.31

eRg + scSNH + (1 | Locality)	468.76	0.68	0.20
year + Within-field position + MFS + scSNH + (1 | Locality)	469.12	0.68	0.30
Within-field position + eRg + MFS + scSNH + (1 | Locality)	469.22	0.68	0.30
Within-field position + scSNH + (1 | Locality)	469.40	0.68	0.19
year + Within-field position + eRgP + MFS + scSNH + (1 | Locality)	469.58	0.68	0.34
year + eRgP + eRg + MFS + scSNH + (1 | Locality)	469.61	0.68	0.34
year + eRg + scSNH + (1 | Locality)	469.70	0.68	0.24
year + eRgP + scSNH + (1 | Locality)	469.94	0.68	0.23
year + Within-field position + scSNH + (1 | Locality)	470.18	0.68	0.23
Within-field position + eRgP + eRg + MFS + scSNH + (1 | Locality)	470.49	0.68	0.33
eRgP + eRg + scSNH + (1 | Locality)	470.94	0.68	0.21
Within-field position + eRgP + scSNH + (1 | Locality)	471.02	0.68	0.21
year + (1 | Locality)	471.03	0.68	0.08
Within-field position + eRg + scSNH + (1 | Locality)	471.04	0.68	0.20
(1 | Locality)	471.12	0.68	0
year + Within-field position + eRg + MFS + scSNH + (1 | Locality)	471.14	0.68	0.31
year + Within-field position + eRg + scSNH + (1 | Locality)	472.04	0.68	0.24
year + eRgP + eRg + scSNH + (1 | Locality)	472.07	0.68	0.24
year + Within-field position + eRgP + eRg + MFS + scSNH + (1 | Locality)	472.07	0.68	0.34
year + Within-field position + eRgP + scSNH + (1 | Locality)	472.28	0.68	0.23
year + eRgP + (1 | Locality)	473.22	0.68	0.08
year + eRg + (1 | Locality)	473.23	0.68	0.08
year + Within-field position + (1 | Locality)	473.25	0.68	0.08
MFS + (1 | Locality)	473.26	0.68	0.00
year + MFS + (1 | Locality)	473.27	0.68	0.08
Within-field position + eRgP + eRg + scSNH + (1 | Locality)	473.28	0.68	0.21
Within-field position + (1 | Locality)	473.29	0.68	0.00
eRg + (1 | Locality)	473.30	0.68	0.00
eRgP + (1 | Locality)	473.31	0.68	0.00
year + Within-field position + eRgP + eRg + scSNH + (1 | Locality)	474.46	0.68	0.24
eRg + MFS + (1 | Locality)	475.29	0.68	0.01
year + eRgP + MFS + (1 | Locality)	475.37	0.68	0.08
eRgP + eRg + (1 | Locality)	475.44	0.68	0.00
year + eRg + MFS + (1 | Locality)	475.45	0.68	0.08
Within-field position + MFS + (1 | Locality)	475.48	0.68	0.00
eRgP + MFS + (1 | Locality)	475.49	0.68	0.00
year + Within-field position + eRgP + (1 | Locality)	475.50	0.68	0.08
year + Within-field position + eRg + (1 | Locality)	475.51	0.68	0.08
Within-field position + eRg + (1 | Locality)	475.52	0.68	0.00
year + eRgP + eRg + (1 | Locality)	475.52	0.68	0.08
Within-field position + eRgP + (1 | Locality)	475.53	0.68	0.00
year + Within-field position + MFS + (1 | Locality)	475.55	0.68	0.08
Within-field position + eRg + MFS + (1 | Locality)	477.57	0.68	0.01

eRgP + eRg + MFS + (1 | Locality)	477.59	0.68	0.01
year + eRgP + eRg + MFS + (1 | Locality)	477.70	0.68	0.08
year + Within-field position + eRgP + MFS + (1 | Locality)	477.71	0.68	0.08
Within-field position + eRgP + eRg + (1 | Locality)	477.72	0.68	0.00
Within-field position + eRgP + MFS + (1 | Locality)	477.76	0.68	0.00
year + Within-field position + eRg + MFS + (1 | Locality)	477.78	0.68	0.08
year + Within-field position + eRgP + eRg + (1 | Locality)	477.86	0.68	0.08
Within-field position + eRgP + eRg + MFS + (1 | Locality)	479.92	0.68	0.01
year + Within-field position + eRgP + eRg + MFS + (1 | Locality)	480.10	0.68	0.08

Model - Wild bees	**AICc**	**R^2 conditional**	**R^2 marginal**
year+ eRgP + SNH + (1 | Locality)	554.62	0.76	0.50
year+ eRgP + (1 | Locality)	554.71	0.76	0.46
year+ MFS + SNH + (1 | Locality)	555.02	0.76	0.49
year+ eRgP + MFS + SNH + (1 | Locality)	555.43	0.76	0.52
year+ eRg + MFS + SNH + (1 | Locality)	556.19	0.76	0.51
year+ Within-field position + eRgP + SNH + (1 | Locality)	556.33	0.77	0.50
year+ Within-field position + eRgP + (1 | Locality)	556.36	0.77	0.46
year+ eRgP + eRg + SNH + (1 | Locality)	556.39	0.76	0.50
year+ Within-field position + MFS + SNH + (1 | Locality)	556.73	0.77	0.49
year+ eRgP + eRg + (1 | Locality)	556.86	0.76	0.46
year+ eRgP + MFS + (1 | Locality)	556.99	0.76	0.46
year+ Within-field position + eRgP + MFS + SNH + (1 | Locality)	557.20	0.77	0.52
year+ eRg + (1 | Locality)	557.27	0.76	0.41
year+ eRg + SNH + (1 | Locality)	557.41	0.76	0.45
year+ eRgP + eRg + MFS + SNH + (1 | Locality)	557.58	0.76	0.52
year+ MFS + (1 | Locality)	557.72	0.76	0.40
year+ Within-field position + eRg + MFS + SNH + (1 | Locality)	557.96	0.77	0.51
year+ Within-field position + eRgP + eRg + SNH + (1 | Locality)	558.16	0.77	0.51
year+ Within-field position + eRgP + eRg + (1 | Locality)	558.57	0.77	0.46
year+ Within-field position + eRgP + MFS + (1 | Locality)	558.70	0.77	0.46
year+ eRg + MFS + (1 | Locality)	558.83	0.76	0.43
year+ Within-field position + eRg + (1 | Locality)	558.93	0.77	0.41
year+ Within-field position + eRg + SNH + (1 | Locality)	559.12	0.77	0.45
year+ eRgP + eRg + MFS + (1 | Locality)	559.22	0.76	0.46
year+ Within-field position + MFS + (1 | Locality)	559.38	0.77	0.41
year+ Within-field position + eRgP + eRg + MFS + SNH + (1 | Locality)	559.41	0.77	0.52
year+ (1 | Locality)	560.06	0.76	0.31
eRgP + SNH + (1 | Locality)	560.46	0.76	0.35
year+ Within-field position + eRg + MFS + (1 | Locality)	560.54	0.77	0.43

year+ Within-field position + eRgP + eRg + MFS + (1 | Locality)	560.99	0.77	0.46
MFS + SNH + (1 | Locality)	561.03	0.76	0.34
eRgP + MFS + SNH + (1 | Locality)	561.16	0.76	0.38
year+ Within-field position + (1 | Locality)	561.66	0.77	0.31
Within-field position + eRgP + SNH + (1 | Locality)	562.12	0.77	0.35
year+ SNH + (1 | Locality)	562.13	0.76	0.31
eRgP + (1 | Locality)	562.14	0.76	0.25
Within-field position + MFS + SNH + (1 | Locality)	562.68	0.77	0.34
eRgP + eRg + SNH + (1 | Locality)	562.70	0.76	0.35
Within-field position + eRgP + MFS + SNH + (1 | Locality)	562.87	0.77	0.38
eRg + MFS + SNH + (1 | Locality)	562.93	0.76	0.34
eRgP + eRg + MFS + SNH + (1 | Locality)	563.52	0.76	0.38
Within-field position + eRgP + (1 | Locality)	563.74	0.77	0.26
year+ Within-field position + SNH + (1 | Locality)	563.79	0.77	0.31
eRgP + eRg + (1 | Locality)	564.33	0.76	0.26
eRgP + MFS + (1 | Locality)	564.39	0.76	0.25
Within-field position + eRgP + eRg + SNH + (1 | Locality)	564.42	0.77	0.35
Within-field position + eRg + MFS + SNH + (1 | Locality)	564.64	0.77	0.35
Within-field position + eRgP + eRg + MFS + SNH + (1 | Locality)	565.29	0.77	0.38
eRg + SNH + (1 | Locality)	565.88	0.76	0.21
MFS + (1 | Locality)	565.93	0.76	0.15
Within-field position + eRgP + eRg + (1 | Locality)	565.98	0.77	0.26
Within-field position + eRgP + MFS + (1 | Locality)	566.04	0.77	0.26
eRgP + eRg + MFS + (1 | Locality)	566.63	0.76	0.26
eRg + (1 | Locality)	566.82	0.76	0.12
Within-field position + MFS + (1 | Locality)	567.53	0.76	0.15
Within-field position + eRg + SNH + (1 | Locality)	567.53	0.77	0.22
eRg + MFS + (1 | Locality)	567.81	0.76	0.16
(1 | Locality)	568.03	0.76	0
Within-field position + eRgP + eRg + MFS + (1 | Locality)	568.35	0.77	0.26
Within-field position + eRg + (1 | Locality)	568.41	0.76	0.12
SNH + (1 | Locality)	569.46	0.76	0.03
Within-field position + eRg + MFS + (1 | Locality)	569.47	0.76	0.16
Within-field position + (1 | Locality)	569.57	0.76	0.00
Within-field position + SNH + (1 | Locality)	571.06	0.76	0.03

Model - Hoverflies	**AICc**	**R^2 conditional**	**R^2 marginal**
Within-field position + MFS + scSNH + (1 | Locality)	558.20	0.46	0.19
year + Within-field position + MFS + scSNH + (1 | Locality)	558.85	0.46	0.22
year + Within-field position + (1 | Locality)	558.89	0.45	0.13
year + Within-field position + MFS + (1 | Locality)	559.86	0.46	0.16

Within-field position + eRg + MFS + scSNH + (1 | Locality)	559.90	0.46	0.20
Within-field position + (1 | Locality)	560.24	0.45	0.05
year + Within-field position + eRgP + (1 | Locality)	560.40	0.46	0.15
Within-field position + eRgP + MFS + scSNH + (1 | Locality)	560.49	0.46	0.19
year + Within-field position + scSNH + (1 | Locality)	560.58	0.46	0.15
year + Within-field position + eRg + MFS + scSNH + (1 | Locality)	560.75	0.46	0.23
Within-field position + MFS + (1 | Locality)	560.80	0.45	0.09
Within-field position + eRgP + (1 | Locality)	561.00	0.45	0.09
year + Within-field position + eRg + (1 | Locality)	561.02	0.45	0.14
year + Within-field position + eRgP + MFS + scSNH + (1 | Locality)	561.08	0.46	0.23
Within-field position + eRgP + scSNH + (1 | Locality)	561.11	0.45	0.13
Within-field position + scSNH + (1 | Locality)	561.37	0.45	0.08
year + Within-field position + eRgP + scSNH + (1 | Locality)	561.46	0.46	0.18
year + Within-field position + eRg + MFS + (1 | Locality)	561.91	0.46	0.17
year + Within-field position + eRgP + MFS + (1 | Locality)	562.23	0.46	0.16
Within-field position + eRg + (1 | Locality)	562.30	0.45	0.06
Within-field position + eRgP + eRg + MFS + scSNH + (1 | Locality)	562.31	0.46	0.20
year + Within-field position + eRg + scSNH + (1 | Locality)	562.37	0.46	0.16
year + Within-field position + eRgP + eRg + (1 | Locality)	562.61	0.46	0.15
Within-field position + eRg + MFS + (1 | Locality)	562.66	0.45	0.10
Within-field position + eRgP + eRg + (1 | Locality)	562.82	0.45	0.10
Within-field position + eRg + scSNH + (1 | Locality)	562.88	0.45	0.10
Within-field position + eRgP + MFS + (1 | Locality)	562.98	0.45	0.09
year + Within-field position + eRgP + eRg + MFS + scSNH + (1 | Locality)	563.22	0.46	0.23
Within-field position + eRgP + eRg + scSNH + (1 | Locality)	563.35	0.45	0.14
MFS + scSNH + (1 | Locality)	563.53	0.39	0.14
year + Within-field position + eRgP + eRg + scSNH + (1 | Locality)	563.86	0.46	0.18
year + MFS + scSNH + (1 | Locality)	564.12	0.39	0.17
year + Within-field position + eRgP + eRg + MFS + (1 | Locality)	564.23	0.46	0.17
year + (1 | Locality)	564.27	0.39	0.08
Within-field position + eRgP + eRg + MFS + (1 | Locality)	564.49	0.45	0.11
eRg + MFS + scSNH + (1 | Locality)	565.17	0.39	0.15
year + MFS + (1 | Locality)	565.20	0.39	0.11
(1 | Locality)	565.68	0.39	0
year + eRgP + (1 | Locality)	565.73	0.39	0.10
eRgP + MFS + scSNH + (1 | Locality)	565.77	0.39	0.14
year + scSNH + (1 | Locality)	565.91	0.39	0.10
year + eRg + MFS + scSNH + (1 | Locality)	565.96	0.39	0.18
MFS + (1 | Locality)	566.19	0.39	0.04
year + eRgP + MFS + scSNH + (1 | Locality)	566.29	0.39	0.17
year + eRg + (1 | Locality)	566.35	0.39	0.09
eRgP + (1 | Locality)	566.38	0.39	0.04
eRgP + scSNH + (1 | Locality)	566.44	0.39	0.08

year + eRgP + scSNH + (1 | Locality)	566.74	0.39	0.12
scSNH + (1 | Locality)	566.75	0.39	0.03
year + eRg + MFS + (1 | Locality)	567.18	0.39	0.12
year + eRgP + MFS + (1 | Locality)	567.50	0.39	0.11
eRgP + eRg + MFS + scSNH + (1 | Locality)	567.52	0.39	0.15
year + eRg + scSNH + (1 | Locality)	567.65	0.39	0.11
eRg + (1 | Locality)	567.68	0.39	0.00
year + eRgP + eRg + (1 | Locality)	567.88	0.39	0.10
eRg + MFS + (1 | Locality)	567.99	0.39	0.05
eRgP + eRg + (1 | Locality)	568.15	0.39	0.05
eRg + scSNH + (1 | Locality)	568.22	0.39	0.05
eRgP + MFS + (1 | Locality)	568.31	0.39	0.04
year + eRgP + eRg + MFS + scSNH + (1 | Locality)	568.37	0.39	0.18
eRgP + eRg + scSNH + (1 | Locality)	568.62	0.39	0.09
year + eRgP + eRg + scSNH + (1 | Locality)	569.07	0.39	0.12
year + eRgP + eRg + MFS + (1 | Locality)	569.44	0.39	0.12
eRgP + eRg + MFS + (1 | Locality)	569.76	0.39	0.06