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# Landscape crop diversity contributes to higher pollination effectiveness and positively affects rapeseed quality in Mediterranean agricultural landscapes

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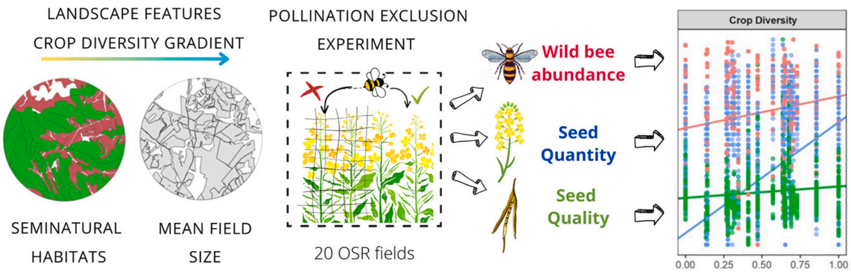
## HIGHLIGHTS

- Few studies relate the crop diversity and the quantity and quality of seed OSRs.
- A total of 20 OSR fields were evaluated across a gradient of crop diversity.
- OSR seed parameters were evaluated with and without insect pollination.
- Crop diversity plays a key role in developing OSR seed quantity and quality.
- The results highlight the importance of considering heterogeneous agricultural systems.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Pollination is crucial for biodiversity and food security. Heterogeneous agricultural landscapes have a positive effect on pollinator abundance and enhance crop production and quality. In this study, we explored the effects of three landscape features (past crop diversity measured as the Equivalent Richness of crop functional Groups in the previous year [ERGp], semi-natural habitat percentage [SNH], and mean field size [MFS]) and pollinator densities (wild bees [WB] and honey bees [HB]) on pollination and seed quantity and quality in rapeseed crops. Surveying the pollinator density in 20 rapeseed fields revealed a positive relationship with ERGp in the landscape. A pollinator exclusion experiment compared bagged and open-pollinated self-compatible rapeseed plants and revealed insect pollination effectiveness (fruits per flower and number of seeds per pod) and seed quality (oil content). Seed parameters were evaluated in relation to pollinator density (WB-HB) and landscape characteristics. The ERGp emerged as a crucial landscape feature that positively impacted WB density. When insect pollinators were excluded, plants exhibited reduced pollination effectiveness and seed quality. Analysis of open-pollinated plants highlighted ERGp as the most influential variable, positively affecting both sets of parameters. The MFS and SNH showed different but important relationships. Total tocopherol and α-tocopherol were positively correlated with pollinator density in HB, whereas WB showed a positive correlation with γ-tocopherol levels. Increased ERGp positively affected pollinator density and pollination effectiveness, thereby improving oilseed rape production quantity and quality. This study provides new insights into agroecosystem management and pollinator-friendly practices.

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## 1. Introduction

Insect pollination is crucial for agricultural productivity and research has shown that this ecosystem service boosts crop yields across a wide range of crops (Bommarco et al., 2012; Dainese et al., 2019; Klein et al., 2007; Potts et al., 2010). The benefits of insect pollination services to agricultural productivity are estimated to range from US $153–577 billion annually (Gallai et al., 2009). Pollinators may also have beneficial effects on food security by increasing the availability of essential macronutrients and micronutrients in the diet (Chaplin-Kramer et al., 2014; Eilers et al., 2011). Pollinator-dependent crops provide 74 % of lipids, 98 % of vitamin C, 70 % of vitamin A, and 34–65 % of vitamin E worldwide (Ellis et al., 2015). Furthermore, the insect pollination of insect-dependent crops produces high-quality yields. For instance, pollinated crops of strawberry, apple and tangerine show higher sugar to acidity ratios, higher calcium content and higher sugar content respectively. Seeds from pollinated rapeseed crop have higher oil content, and pollinated almond trees have lower vitamin E content (Bommarco et al., 2012; Brittain et al., 2014; Garratt et al., 2014; Klatt et al., 2014; Wietzke et al., 2018). Therefore, pollination not only increases production but also improves the crop quality (Gazzea et al., 2023; Prado et al., 2018).

Worldwide, 75 % of the over 100 crop species cultivated rely on or benefit from pollination (Klein et al., 2007). Moreover, the cultivation area for crops that do not depend on pollinators only grew by 17.3 %, whereas the area for pollinator-dependent crops expanded by 136.9 %, which also increased the demand for pollinators and pollination. Despite significant increases in their reliance on pollinators, European countries have not exhibited increased crop diversity yet (Aizen et al., 2019).

The ecosystem service of pollination is declining owing to agricultural intensification at the farm level. This is exacerbated by the reduction of semi-natural areas and crop diversification at the landscape level (Mandelik et al., 2012). If the global trend of increasingly intensive agriculture relying on pollinators continues, there will be a major mismatch in pollination demand, which could worsen the current food security scenario in terms of crop quantity and quality (Chaplin-Kramer et al., 2014; Smith et al., 2015). Therefore, to guarantee stable crop yields, functional pollinator communities must be preserved urgently (Wietzke et al., 2018).

Landscape characteristics, such as the extent of semi-natural habitats, agricultural and urban areas, and crop diversity, have been shown to influence crop yield and biochemical processes (Cunha et al., 2023; Halinski et al., 2020; Magrach et al., 2023; Pioltelli et al., 2024a). In agricultural landscapes, for example, areas with higher crop diversity help maintain more diverse sets of pollinators and, as a result, more efficient and stable pollination services (Aguilera et al., 2020; Hass et al., 2018a, 2018b). Numerous studies have been conducted to assess potential pollination services by analysing the abundance and diversity of pollinator species and agricultural production, or through the interaction of plants and pollinators (Bartomeus et al., 2014; Bommarco et al., 2012; Cunha et al., 2023; Holzschuh et al., 2016; Perrot et al., 2018). Furthermore, the functional role of crop diversity and past crop diversity at the landscape level has been documented, owing to their potential capacity to provide a greater abundance and density of pollinators (Aguilera et al., 2020; Neira et al., 2024). However, knowledge of the relationships between crop diversity, pollinator abundance, pollination effectiveness, and the quality of agricultural production at the landscape scale remains limited.

Oilseed rape (OSR) (*Brassica napus* L.) is a valuable, economically important, and rapidly expanding crop. This crop is recognized as a mass flowering crop that attracts a high density of pollinators from seminatural zones when it occupies a low proportion of the landscape (Holzschuh et al., 2016, 2011). During its flowering stage, and when it covers <10 % of the landscape, it can concentrate up to 55 % of pollinator species from grasslands (Magrach et al., 2018). OSR crops are mostly self-pollinated, but benefit from wind and insect pollination (Bartomeus et al., 2014; Beyer et al., 2021; Bommarco et al., 2012). Seed quality is measured by parameters such as oil content (%), chlorophyll content and moisture, which are routinely used by agricultural product traders to assess the quality of OSR seeds and indicate the quality of the resulting oil (Australian Oilseeds Federation, 2011). Oil extracted from OSR seeds has been used in the food industry for human and animal consumption and is considered a rich source of antioxidants and health-promoting bioactive compounds, such as tocopherols and carotenoids, owing to their nutritional value as vitamin E and provitamin A, respectively. Conversely, high chlorophyll content reduces the price of oil because it decreases durability and negatively alters the colour of the extracted oil (Bommarco et al., 2012; Schneider, 2005). However, studies regarding the association between landscape crop diversity and quantity (e.g., seeds per pod) and quality (e.g., antioxidants or plant pigments) of seeds from insect-pollinated OSR have not yet been conducted in Mediterranean climates.

We conducted a pollinator exclusion experiment and assessed wild pollinator and honeybee (HB) densities in 20 rapeseed fields in central Catalonia across a gradient of crop diversification, abundance of seminatural areas, and mean field sizes. We evaluated the influence of the agricultural landscape on the density of pollinators and the effectiveness of pollinators visiting rapeseed flowers on the quantity and quality parameters of OSR seeds. This approach allows for an interdisciplinary understanding of the effects of the agricultural landscape on pollinators, and consequently, on the qualitative and quantitative characteristics of rapeseeds. We hypothesised that: i) OSR fields in landscapes with higher past crop diversity receive more visits from wild bees (WB), and ii) the amount and quality of OSR fruits pollinated by insects are higher than those produced by self-pollination; consequently, iii) past crop diversity in an agricultural area affects both the quantity and quality of OSR seeds, with wild bees playing an important role.

## 2. Materials and methods

### 2.1. Study fields and landscape metrics

During the years 2021 and 2022, we chose 20 conventional arable fields seeded with different varieties of OSR (*Brassica napus* L.), in total (10 per year), each field in a dryland cereal region situated in Central Catalonia, in the NE Spain (41°24′–42°05′N; 1°05′–2°05′E) (Fig. 1A). All localities were at least 2 km apart to prevent any two OSR fields from being visited by the same pollinator pool (Holzschuh et al., 2016; Westphal et al., 2003). The agricultural environment is characterised by the dominance of dryland arable crops and woody crops, whereas uncultivated areas are dominated by forests, shrublands, and grasslands (Departament d'Acció Climàtica, Alimentació i Agenda Rural, 2023).

A circular area with a radius of 1000 m was chosen around each rapeseed field to characterise the landscape of each locality, as it has been shown that the majority of pollinator feeding flights occur within this distance (Holzschuh et al., 2011; Steffan-Dewenter and Kuhn, 2003). Landscape heterogeneity was characterised by three components, two of which were associated with its composition: (1) the equivalent crop richness of the past year (ERGp), which corresponds to the effective number of crop functional groups of crops computed as the exponential of the Shannon diversity of functional groups of crops (e.g. legumes, oilseeds, sweet fruits, cereals) (Neira et al., 2024); (2) the percentage of land covered by seminatural habitats (SNH); and (3) one component associated with its configuration, the mean field size (MFS). The localities were chosen according to an ERGp gradient, with a maximum of 10 % agricultural area cultivated with rapeseed crops, to guarantee the effect of bee concentration (Fig. 1B) (Holzschuh et al., 2011; Magrach et al., 2023). The composition and structure of the landscape in each locality were characterised using spatial data from 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

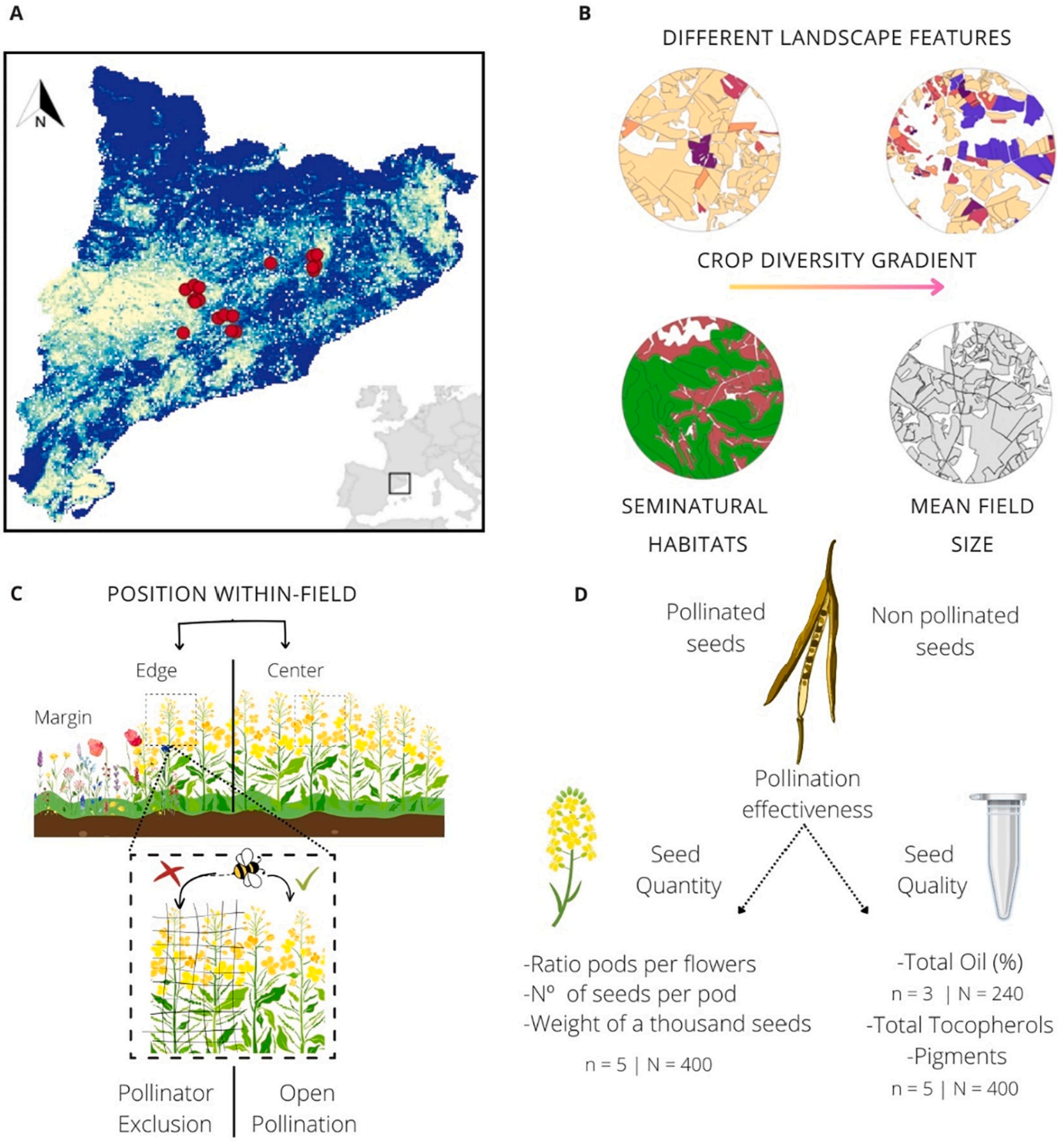


**Fig. 1.** Study fields and experimental design. A) Map of Catalonia (NE of Spain) and the distribution of the 20 localities. The blue-yellow gradient represents the percentage of agricultural land. Information is available in the Cartografia dels Hàbitats de Catalunya, v.2 (Departament de Territori i Sostenibilitat, 2018). B) Representation of the 1-km radius buffer zone of the selected localities in a gradient of crop diversity; representation of the other characteristics of the agricultural landscape evaluated; seminatural habitats; and mean field size. C) Scheme of the pollinator exclusion experiment design within each rapeseed field. D) Methodological diagram of the use of samples and their respective parameters. n: Number of samples per field, N: Total number of samples.

package 'sf' (Pebesma, 2018).

### 2.2. *Pollination assessment*

A pollinator exclusion experiment was set up prior to flowering in the twenty rapeseed fields. Within each field, crop plants in two within-field positions (centre and edge) were subjected to two different pollination treatments: open pollination (OP), which included plants whose inflorescences could be pollinated through all vectors (wind and insects), and pollinator-excluded plants (EP), whose contact with insects was limited (Fig. 1) (Bommarco et al., 2012; Perrot et al., 2018). In each within-field position, five plants × two pollination treatments from ten size-equivalent plants, split into five pairs 18 m apart, were chosen at random in an area of 75 m × 2 m (10 inflorescences × two within-field positions × 20 fields = 400 inflorescences). To prevent pollinating insects from visiting EP plants, a fine mesh nylon bag (0.8 mm × 0.8 mm) was installed around each inflorescence from randomly selected plants within each pair. Although inflorescences from OP plants were available for both self-pollination and wind and insect pollination, insect pollination was completely excluded from inflorescences from EP plants (Fig. 1D). A previous evaluation inside and outside the mesh nylon bag did not reveal any significant differences in photon flux ($p > 0.05$) (Table S1) that could have an impact on the physiological responses of OSR plants. In both cases, the levels of photon flux are higher than what is considered to be shadow stress (Wang et al., 2023).This experimental approach, which allows for both self-pollination and wind pollination, was developed in previous field studies (Bartomeus et al., 2014; Beyer et al., 2021; Bommarco et al., 2012; Islam et al., 2022). Plants from both treatments were collected one day before the crop was harvested in July to ensure pod ripening in the field (Beyer et al., 2021; Bommarco et al., 2012). Plant material collected were stored in paper bags at room temperature (22–26 °C) until they were processed, and then preserved in cold conditions for future analysis.

### 2.3. Pollinator evaluation

A pollinator survey was conducted in each rapeseed field between April and May (2021 and 2022). Two parallel transects of 150 $m^2$ (75 m × 2 m) were established in each field, one at the centre and the other at the edge of the field. To determine the densities of WBs and HBs, the number of contacts with rapeseed flowers was recorded for 15 min per transect (Holzschuh et al., 2016). The surveys were conducted on two different days during the peak flowering period under fair weather no rain, temperature above 15 °C, low wind speed. The total sampling effort was 15 min/transect × two transects/field/day × two days = 60 min/ field.

### 2.4. Pollination effectiveness

To quantify the pollination effectiveness, three parameters were estimated for each of the 400 OSR inflorescences: (1) pods per flower ratio (PPF), (2) number of seeds per pod (NSP), and (3) thousand seed weight (TSW). The total number of pods was divided by the number of flowers in each inflorescence to calculate PPF as an indicator of pollination effectiveness. NSP was obtained from a mean of five pods per infructescence (a total of 2000 pods). The TSW was calculated using the following formula: 1000 × (weight of all seeds from the infructescence) / (average number of seeds per pod × total pods).

### 2.5. Phytochemical analyses and quality of seeds

Three analyses were performed to assess the quality of OSR seed production: (1) percentage of oil content in the seeds, (2) tocopherol composition and quantification, and (3) quantification of total chlorophyll and carotenoids. Oil content was determined using a modified gravimetric protocol (Bligh and Dyer, 1959). Seeds from three infructescence were randomly chosen for each pollination treatment condition and within-field position (centre/edge) per field ($N = 240$). Seeds from each infructescence were crushed and 100 mg of each sample was weighed. One millilitre of the extraction solvent (chloroform:methanol, 2:1 *v*/v) was added to each sample and an ultrasonication bath was applied for 15 min before centrifugation at 5000 rpm for 10 min. The supernatant was extracted and transferred to glass vials that had previously been weighed. The solvent extraction procedure was repeated three times until a white pellet was obtained. The glass vials containing the supernatant were exposed to nitrogen until the solvent evaporated and the weight was stabilised. The oil content corresponded to the percentage of the final weight minus the initial weight of the vial over the weight of the initial OSR sample.

Tocopherols were analysed following the procedure described by Amaral et al. (2005). Seeds from five infructescences were randomly chosen for each pollination treatment condition and each within-field position (centre/edge) per field ($N = 400$). Cold extraction was performed as follows: samples were kept cold using ice, and extraction products were extracted with 100 % methanol containing 0.01 % butylhydroxytoluene on 30 mg of seeds from each sample, which had previously been crushed and placed in Eppendorf tubes (2 mL). Methanol (400 μL) was then added to each sample, and ultrasonication bath was applied for 30 min, with the samples passing through a vortex before and after this step, and finally the samples were centrifuged at 10,000 rpm for 10 min. The extraction procedure was repeated two more times until a completely white pellet was obtained, and the final supernatant was separated into two aliquots: one for tocopherols analysis and the other one for total pigment determination. Extracts were filtered using single-use 0.45-μm polytetrafluoroethylene hydrophobic filters and a portion was transferred to glass vials for analysis using high-performance liquid chromatography. A Waters 600 controller pump, Waters 717 plus autosampler, and Jasco FP-1520 fluorescence detector (Jasco, Tokyo, Japan) were used. Tocopherol compounds were separated on a normal-phase column (Inertsil SIL-100 A, 5 μm, 3.0 × 250 mm, GL Sciences, Tokyo, Japan) with an isocratic mobile phase of n-hexane and 1,4-dioxane (95.5/4.5; *v*/v). The flow rate was 0.7 $mL·min^{-1}$ and the injection volume was 10 μL. The excitation wavelength was 295 nm, and the emission wavelength was 330 nm for fluorescence detection. A calibration curve with authentic standards using a concentration range from 0.1 to 5 μg/mL (Sigma-Aldrich, Steinheim, Germany) was used to quantify the compounds.

The second aliquot was used for dual-beam ultraviolet/visible spectrophotometric analyses of chlorophylls a and b, and total carotenoids using a CE Aquarius UCE7400 (Cecil Instruments Ltd., Cambridge, United Kingdom). To quantify chlorophylls a and b, as well as total carotenoids, we measured absorbance at 750 nm, 665.2 nm, 652.4 nm, and 470 nm and applied the equations with absorption coefficients as described by Lichtenthaler and Buschmann (2001).

### 2.6. Statistical analysis

To analyze the obtained data, we used Generalized Mixed Linear Models (GLMMs) with the ‘glmmTMB’ package (Brooks et al., 2017). First, to check for significant correlations, a Spearman rank's correlation analysis was conducted between the landscape characteristics and the densities of WBs, HBs, and total bees (Fig. S1). A strong correlation was identified between the MSF and ERGp. Therefore, a sequential regression approach (Graham, 2003) was used to create a new purged explanatory variable by reciprocally subtracting the common variation from the MFS to the ERGp. This approach allowed the inclusion of both variables in the model. We then used the variance inflation factor (VIF) to test for potential collinearity between these explanatory variables (Zuur et al., 2010); however, the VIF indicated low multicollinearity in all cases (Table S2). To analyze WB density and its relationship with the agricultural landscape, the landscape metrics ERGp, MFS, and SNH were treated as continuous explanatory variables (scaled to minimum = 0 and maximum = 1), whereas within-field position (edge and centre) and year were used as categorical explanatory variables.

In the pollinator exclusion experiment, the total pollinator density (the sum of WB and HB) was treated as a continuous variable. Pollination treatment (OP or EP), within-field position (edge or centre), and year were the categorical variables. We also considered the interactions between the total density of bees and pollination treatment, and the interaction between the total density of bees and the within-field position. The interaction term is needed when analysing the effect of total density of bees on both EP and OP plants in the same model, as it is expected a lack of effect in EP but a significant effect in OP. The interaction term allows us to attribute any effect to the total density of bees and not to wind pollination or any other uncontrolled effect. Crop variety was included as a random effects factor. Finally, to test the influence of the agricultural landscape and pollinators on the pollination effectiveness and the quality of OSR seeds of OP OSR plants, the agricultural landscape variables (ERGp, MFS, and SNH) were scaled and treated as continuous variables as in the first analysis. Bee densities (WB and HB) were log transformed before analysis, to reduce variability at the higher end of the variable and improve the homogeneity of distribution of this explanatory variable. We used the OSR variety as a random effect variable.

In these three analyses, we used the ‘dredge’ function in the ‘MuMIn’ package (Bartoń, 2023) to test multiple hypotheses simultaneously across the models. We investigated all possible combinations for each dataset. For each model (i), we computed the Akaike information criterion corrected for small sample sizes (AICc), and we ranked and calculated relative Akaike weights (w) (Akaike, 1998; Burnham and Anderson, 2002). Then, a relative weight of evidence for each model ($w_i$) can be interpreted as the probability of model a being the best approximating model from the entire set of candidate models. The sum of the weights ($w_i$) of all possible models is scaled to 1. We calculated the confidence sets for each response variable, which are the smallest subsets of candidate models for which the sum of $w_i$ equals 0.95, and we averaged the entire set. For each variable included in the set of candidate models, its relative importance is calculated based on its contribution to explaining the variability in the response variable. We report all predictor variables, considering as relevant all variables that have a relative importance ($\Sigma w_i$) >0.5, and 95 % confidence intervals (CI) as critical tools for assessing variable effects. We inspected residual plots to validate model assumptions and calculated the marginal ($R^2_m$) and conditional ($R^2_c$) $R^2$ values (Nakagawa et al., 2017). Furthermore, in the case only one model had a weight of >0.95, we calculated the estimates and *p*-values. Statistical analyses were performed using R software version 4.1.2.

## 3. Results

### 3.1. Agricultural landscape effects on pollinators

In the 20 OSR fields, 2592 HBs and 992 WBs were recorded. The total number of WBs belonging to the genus *Bombus* was 231, whereas 761 belonged to other WB genera. The average model for WBs indicated that ERGp influenced them positively, with a relative importance ($\Sigma w_i$) of 0.73, the unique feature of the landscape was supported by the CI. The second most important landscape feature was MFS ($\Sigma w_i = 0.68$) with a negative effect. Both features showed a clear effect. Within-field position displayed higher pollinators density in the edge than in field centres, but this effect had a relative importance ($\Sigma w_i$) of 0.43, whereas SNH ($\Sigma w_i = 0.28$) had a negative effect. Both features showed an unclear effect and without support from their CIs (Fig. 2).

### 3.2. Pollinator exclusion effects on seed quantity

The parameters associated with seed quantity were responsive to both pollination treatment and pollinator density (Table 1). The observed PPF in rapeseed fields was explained by a single model ($w_i$ > 0.95) encompassing all variables studied. Within-field position and pollinator density exhibited negative effects ($P < 0.001$), thereby decreasing the PPF. The interaction between total pollinator density and within-field position a positive influence ($P < 0.001$), decreasing less PPF ratio in edge plants than in centre plants with higher pollinator density. In contrast, plants subjected to the pollination treatment in the interaction with pollinator densities demonstrated a statistically significant positive effect ($P < 0.001$) in OP plants. Inflorescences from OP plants produced 39 % more pods per flower than that produced by EP plants ($P < 0.001$) (Fig. 3A).

The NSP, as indicated by the average model (Table 1), decreased in response to pollinator density. This negative response was more pronounced at the edge of the field than at the centre. Both variables had a relative importance of $\Sigma w_i = 1.00$. However, when both variables interacted (TD:P in Table 1), we observed a positive effect ($\Sigma w_i = 0.62$), indicating that the NSP of plants at the edge decreased less than centre plants in response to increasing pollinator density. The pollination treatment revealed that OP inflorescences had a higher NSP than EP ($\Sigma w_i = 1.00$). The pollination treatment also revealed that OP

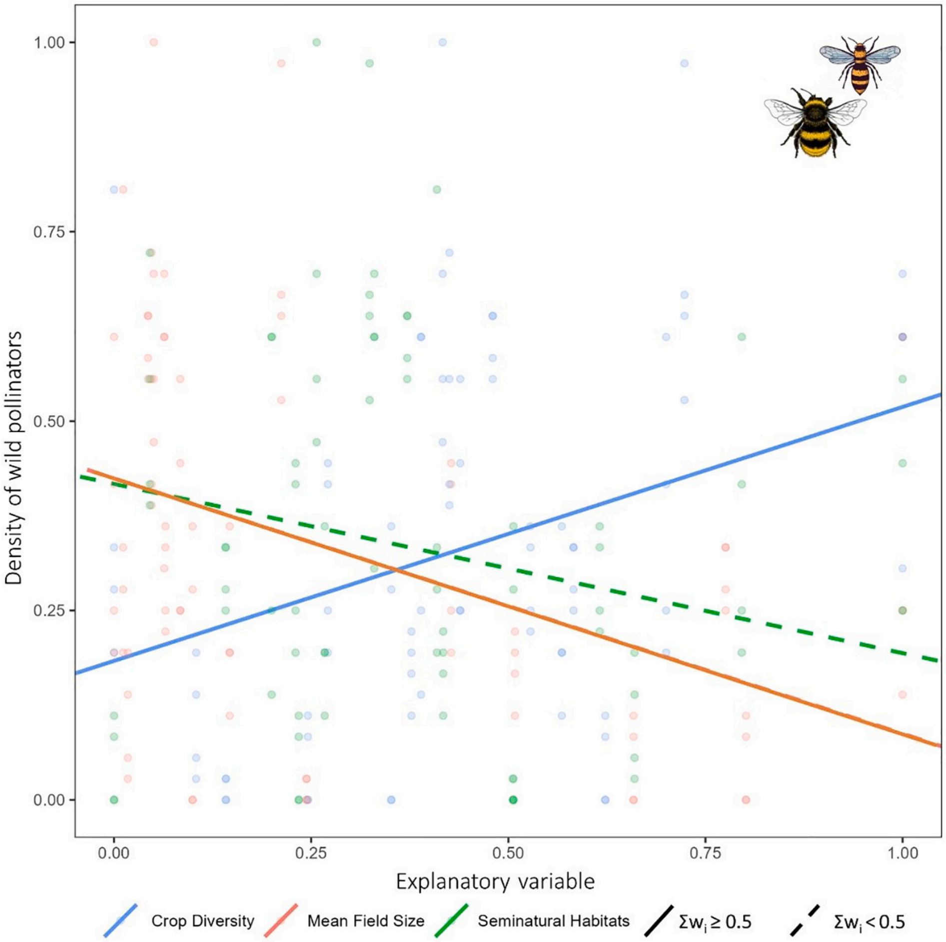


**Fig. 2.** Relationship between agricultural landscape variables and density of wild pollinators. Lines represent the model effects for each landscape metric of the agricultural landscape individually and were obtained from the average model of the multimodel analysis. Relative importances greater than or equal to 0.5 are represented with solid lines. Relative importances <0.5 are represented with dashed lines.

**Table 1**
Estimates and relative importance ($\Sigma w_i$) for each predictor in the average models obtained through multimodel inference or estimate and p-values when it corresponds to a single model from the pollinator exclusion experiment. For each fixed effect factor, confidence intervals (CI at 95 %) are provided. Bold numbers indicate relevant variables. Total pollinator density (TD), pollination treatment (PT), within-field position (P), (TD:PT): interaction between total pollinator density and pollination treatment, (TD:P): interaction between total pollinator density and within-field position.

| Quantity parameters | | Estimate | $\Sigma w_i$/ p-value | CI | |
|---|---|---|---|---|---|
| | | | | Lower | Upper |
| Pods per flower (PPF) (only one model) | Total pollinator density | **−0.000** | **P < 0.001** | **−0.001** | **−0.000** |
| | Pollination treatment (Open vs. Exclusion) | **0.250** | **P < 0.001** | **0.235** | **0.265** |
| | Within-field position (edge vs centre) | **−0.063** | **P < 0.001** | **−0.076** | **−0.049** |
| | TD:PT | **0.001** | **P < 0.001** | **0.000** | **0.001** |
| | TD:P | **0.000** | **P < 0.001** | **0.000** | **0.000** |
| Nª seeds per pod (NSP) | Total pollinator density | **−0.047** | **1.00** | **−0.063** | **−0.031** |
| | Pollination treatment (open vs. exclusion) | **3.236** | **1.00** | **2.354** | **4.118** |
| | Within-field position (edge vs centre) | **−3.976** | **1.00** | **−4.883** | **−3.070** |
| | TD: PT | **0.045** | **1.00** | **0.030** | **0.060** |
| | TD:P | **0.013** | **0.62** | **−0.002** | **0.027** |
| Thousand seed weight | Total pollinator density | **0.002** | **0.67** | **−0.001** | **0.004** |
| | Pollination treatment (open vs. exclusion) | **0.650** | **1.00** | **0.506** | **0.795** |
| | Within-field position (edge vs centre) | **−0.076** | **0.82** | **−0.158** | **0.006** |
| | TD: PT | **−0.002** | **0.51** | **−0.004** | **0.001** |
| | TD:P | 0.000 | 0.13 | −0.002 | 0.002 |
| Oil content (%) | Total pollinator density | **−0.012** | **1.00** | **−0.035** | **0.011** |
| | Pollination treatment (open vs. exclusion) | **2.328** | **1.00** | **0.959** | **3.698** |
| | Within-field position (edge vs centre) | **−0.750** | **1.00** | **−2.153** | **0.654** |
| | TD:PT | **0.044** | **1.00** | **0.021** | **0.066** |
| | TD:P | **−0.024** | **1.00** | **−0.047** | **−0.001** |
| Total tocopherols | Total pollinator density | **0.167** | **0.63** | **−0.07** | **0.404** |
| | Pollination treatment (open vs. exclusion) | 3.308 | 0.29 | −7.283 | 13.899 |
| | Within-field position (edge vs centre) | **15.947** | **0.92** | **−1.415** | **33.309** |
| | TD:PT | −0.025 | 0.29 | −0.278 | 0.229 |
| | TD:P | −0.255 | 0.43 | −0.517 | 0.008 |
| α-Tocopherol | Total pollinator density | **9.812** | **0.80** | **−0.596** | **20.220** |
| | Pollination treatment (open vs. exclusion) | **−9.947** | **0.67** | **−21.046** | **1.152** |
| | Within-field position (edge vs centre) | **19.808** | **1.00** | **8.676** | **30.985** |
| | TD:PT | −0.214 | 0.08 | −11.267 | 10.839 |
| | TD:P | **−11.987** | **0.61** | **−23.360** | **−0.382** |
| γ-Tocopherol | Total pollinator density | **2.350** | **1.00** | **−1.451** | **6.151** |
| | Pollination treatment (open vs. exclusion) | **17.254** | **1.00** | **13.109** | **21.398** |
| | Within-field position (edge vs centre) | **−15.463** | **1.00** | **−19.612** | **−11.313** |
| | TD:PT | −7.981 | 0.18 | −4.005 | 4.290 |
| | TD:P | **−0.142** | **1.00** | **−12.279** | **−3.683** |
| Chlorophylls | Total pollinator density | **−0.002** | **0.61** | **−0.007** | **0.003** |
| | Pollination treatment (open vs. exclusion) | **−0.019** | **1.00** | **−0.025** | **−0.013** |
| | Within-field position (edge vs centre) | **−0.005** | **0.56** | **−0.011** | **0.001** |
| | TD:PT | −0.004 | 0.27 | −0.010 | 0.002 |
| | TD:P | – | – | – | – |
| Carotenoids | Total pollinator density | −0.002 | 0.42 | −0.005 | 0.001 |
| | Pollination treatment (open vs. exclusion) | **−0.014** | **1.00** | **−0.017** | **−0.01** |
| | Within-field position (edge vs centre) | 0.001 | 0.30 | −0.002 | 0.005 |
| | TD:PT | 0.002 | 0.08 | 0.002 | −0.002 |
| | TD:P | 0.002 | 0.04 | −0.002 | 0.005 |

inflorescences also showed a lower decrease of NSP in response to increasing total pollinator density than EP inflorescences ($\Sigma w_i = 1.00$) (TD:PT in Table 1). EP plant inflorescences exhibited a 15 % lower of NSP than those from OP plants ($P < 0.001$) (Fig. 3B).

The average model for the TSW (Table 1) shows an increased trend for both the total pollinator density ($\Sigma w_i = 0.67$) and the pollination treatment, where OP plant seeds were heavier ($\Sigma w_i = 1.00$). Both variables exhibited clear effects. Conversely, the within-field position ($\Sigma w_i = 0.82$) had negative effects, indicating that the edge plants show lower TSW compared with those at the centre of the field. Regarding the interactions, only the interaction between total pollinator density and pollination treatment showed a negative and clear effect ($\Sigma w_i = 0.51$) (TD:PT in Table 1), indicating that OP plants exhibited a decrease in TSW relative to EP plants in the presence to increasing total pollinator density. Notably, seeds from the EP plant inflorescences weighed 40 % less than those from OP plants open to insect visits ($P < 0.001$) (Fig. 3C).

### *3.3. Pollinator exclusion effects on seed quality*

The quality parameters of the rapeseed seeds primarily showed responsiveness to pollination treatment and location within the field (Table 1). The analysis of oil content (%) in rapeseed seeds reveals a positive response for OP plants of the pollination treatment ($\Sigma w_i =$

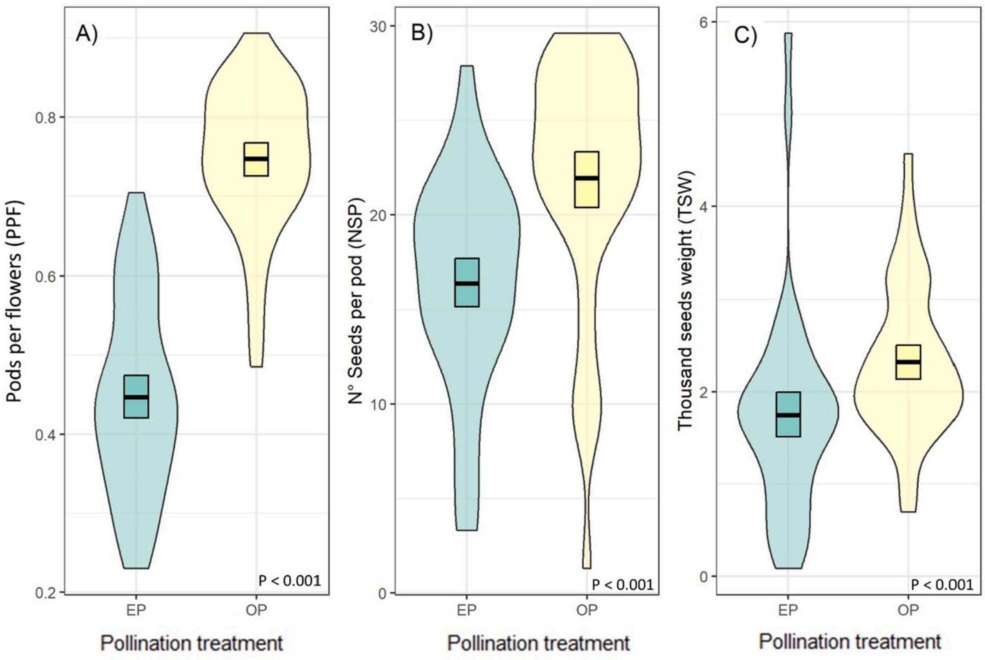


**Fig. 3.** Effects of the pollination treatment on (A) pods/flowers, (B) the number of seeds per pod and (C) the thousand seed weight. The 95 % confidence intervals for treatments are shown in boxes inside of each violin graph. Results of statistical comparison among inflorescences from pollinator-excluded plants (EP) and open-pollinated plants (OP) are indicated below each graph.

1.00), showing more oil content than that in EP plants, and this finding is supported by its confidence interval. The total density of pollinators and the position in the field had a negative effect ($\Sigma w_i = 1.00$). Whereas the interaction between the pollinator density and within-field position (TD: P in Table 1) exhibits a negative effect ($\Sigma w_i = 1.00$) indicating that the seeds of plants on the field edge have even less oil content in the presence of a higher density of pollinators than plants in the field centre. A positive effect is observed in the interaction between total pollinator density and pollination treatment (TD:PT in Table 1) ($\Sigma w_i = 1.00$), showing that OP plant seed oil content increases as pollinator density increases, and both interactions are supported by their confidence interval. Notably, seeds from the inflorescences of EP plants contained 10 % less oil than those from OP plants ($P < 0.001$) (Fig. 4A).

The average model for total tocopherols in OSR seeds indicates an increase in relation to within-field position showing more content at the edge ($\Sigma w_i = 0.92$). The tocopherol content also increased as the pollinator density increased ($\Sigma w_i = 0.63$), and although its confidence intervals encompass zero, it exhibits clear positive effects (Table 1). Overall, pollination treatment doesn't show a clear effect ($\Sigma w_i = 0.29$). Seeds from the inflorescences of EP and OP plants did not show any

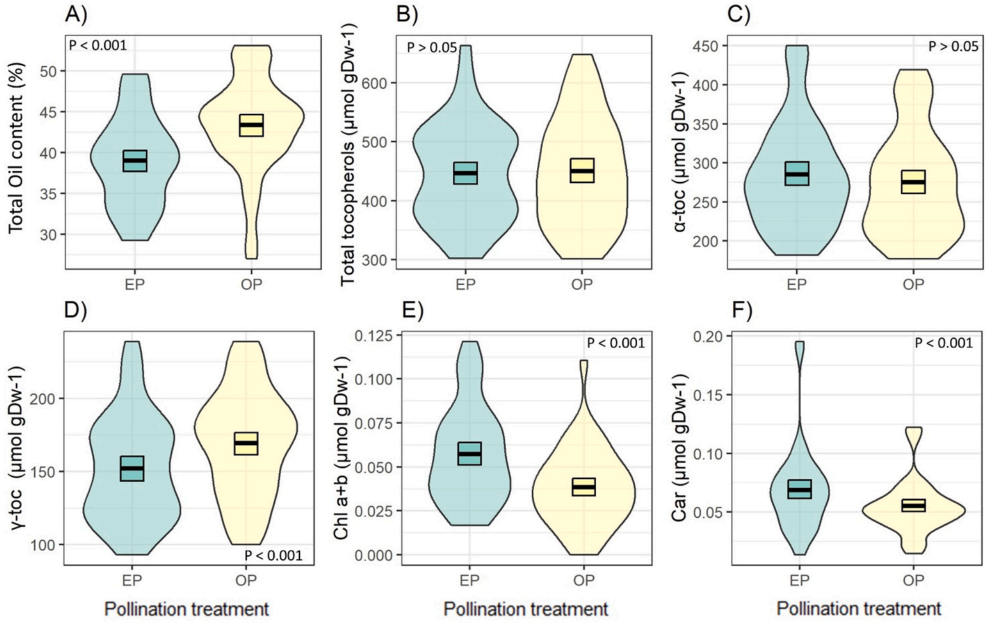


**Fig. 4.** Effects of the pollination treatment on (A) seed oil content (%), (B) total tocopherols (α-toc + γ-toc), (C) α-toc, (D) γ-toc, (E) chlorophyll (a + b) and (F) carotenoids. The 95 % confidence intervals for treatments are shown in boxes inside each violin graph. *P*-values of statistical comparison among inflorescences from EP and OP plants are indicated in each graph.

significant differences in total tocopherol content ($P > 0.05$) (Fig. 4B).

Tocopherol composition shows two predominant tocopherols, α- and γ-tocopherol. The α-tocopherol content was higher in plants from field edge than in plants from field centre ($\Sigma w_i = 1.00$, Table 1). However, we detected an important interaction with total pollinator density ($\Sigma w_i = 0.61$, TD:P in Table 1), causing a steeper positive response of α-tocopherol to total pollinator density in the field centre than in field edge (i.e. total pollinator density effect on α-tocopherol content is higher in the field centres than in field edges). Each variable was supported by its respective confidence intervals. The α-tocopherol content increased in response to increased pollinator density ($\Sigma w_i = 0.80$) and pollination treatment ($\Sigma w_i = 0.67$). There was no difference between OP and EP plants in the α-tocopherol content ($P > 0.05$) (Fig. 3C). For γ-tocopherol, the variables carrying the greatest relative importance, as outlined by the average model (Table 1), encompassed the total pollinator density, within-field position, their interaction, and the pollination treatment, all boasting a relative importance of $\Sigma w_i = 1.00$, with clear effects. The γ-tocopherol content increased as pollinator density increased ($\Sigma w_i = 1.00$) and showed higher levels in plants from the centre. Their interactions exhibited negative trends, indicating that the increase was smaller in the edge plants than in the centre (TD:P in Table 1). In seeds from OP plants, γ-tocopherol content was also higher, but the interaction with pollinator density had no clear effect (TD:PT in Table 1). The γ-tocopherol content of seeds from OP plants was 10 % higher than that from EP plants ($P < 0.001$) (Fig. 4D).

The total chlorophylls, as indicated by the average model, only showed a relationship with the pollination treatment ($\Sigma w_i = 1.00$) which is supported by the confidence interval. Seeds from OP plants have a lower chlorophyll content than those from EP plants. In contrast, the remaining variables had an unclear effect. Seeds from the inflorescences of EP plants contained 60 % more total chlorophyll than those from the inflorescences of OP plants ($P < 0.001$) (Fig. 4E). Total carotenoids were primarily influenced by the pollination treatment ($\Sigma w_i = 1.00$), as per the average model (Table 1). This effect was supported by its confidence interval, which indicated that seeds from OP plants had a lower carotenoids content than those from EP plants. The remaining variables exhibited lower relative importance, and their confidence interval contained zero, with a tendency towards symmetry; therefore, we could not consider their effects. Seeds from EP plants had 20 % higher total carotenoids content than those from OP plants ($P < 0.001$) (Fig. 4F).

### *3.4. Agricultural landscape and pollinator density affected pollination effectiveness and rapeseed seeds quality*

The average model indicated that the pollination effectiveness parameters of the OP treatment seeds responded to agricultural landscape and pollinator density variables (Table 2 and Fig. 5). The average model for PPF revealed that ERGp ($\Sigma w_i = 0.71$) and SNH ($\Sigma w_i = 0.95$) were the variables with the highest relative importance, both corroborated by their confidence intervals (Table 2). PPF increased in plants from landscapes with higher crop diversity and decreased with increasing SNH proportion in the agricultural landscape. In contrast, MFS, WB and HB densities did not have a clear effect. Crop diversity (ERGp) was the most important ($\Sigma w_i = 1.00$) variable influencing NSP, with greater crop diversity resulting in increased NSP. MSF ($\Sigma w_i = 0.60$) and SNH ($\Sigma w_i = 0.67$) presented lower relative importance, and although their confidence intervals included zero, they also showed clear effects, thereby increasing NSP in landscapes with small field sizes or with a higher proportion of SNH. The WB ($\Sigma w_i = 0.25$) and HB ($\Sigma w_i = 0.41$) densities did not have a clear effect. For the TSW, the average model revealed that only SNH ($\Sigma w_i = 1.00$) had effects on TWS, which was the variable with the highest relative importance, with a positive effect supported by their respective confidence intervals. This indicated that the greater the proportion of SNH in the agricultural landscape, the higher the TSW.

The percentage of oil content in the seeds was explained by an

**Table 2**
Estimates and relative importance ($\Sigma w_i$) for each predictor in the average models obtained through multimodel inference or estimate and *p*-value when it corresponds to a single model from the analysis of landscape effects on open pollination treatments plants. For each fixed effect factor, confidence intervals (CI) (95 %) are provided. Bold numbers indicate relevant variables.

| Quantity parameters | | Estimate | $\Sigma w_i$ | CI | |
|---|---|---|---|---|---|
| | | | | Lower | Upper |
| Pods per flower (PPF) | Wild bees (WB) | 0.008 | 0.32 | −0.010 | 0.026 |
| | Honeybees (HB) | 0.005 | 0.24 | −0.013 | 0.022 |
| | Crop diversity (ERGp) | **0.017** | **0.71** | **0.000** | **0.034** |
| | Mean field size (MFS) | −0.016 | 0.49 | −0.037 | 0.005 |
| | Seminatural habitats (SNH) | **−0.031** | **0.95** | **−0.053** | **−0.009** |
| | Within-field position (edge vs centre) | 0.000 | 0.19 | −0.025 | 0.024 |
| Nª seeds per pod (NSP) | Wild bees (WB) | −0.516 | 0.25 | −1.842 | 0.810 |
| | Honeybees (HB) | −0.748 | 0.41 | −1.965 | 0.469 |
| | Crop diversity (ERGp) | **2.789** | **1.00** | **1.522** | **4.056** |
| | Mean field size (MFS) | **−1.603** | **0.60** | **−3.587** | **0.381** |
| | Seminatural habitats (SNH) | **1.492** | **0.67** | **−0.085** | **3.070** |
| | Within-field position (edge vs centre) | −0.004 | 0.18 | −1.536 | 1.528 |
| Thousand seed weight | Wild bees (WB) | −0.026 | 0.22 | −0.168 | 0.115 |
| | Honeybees (HB) | −0.063 | 0.29 | −0.204 | 0.079 |
| | Crop diversity (ERGp) | 0.016 | 0.23 | −0.136 | 0.168 |
| | Mean field size (MFS) | 0.109 | 0.36 | −0.100 | 0.318 |
| | Seminatural Habitats (SNH) | **0.440** | **1.00** | **0.270** | **0.610** |
| | Within-field position (edge vs centre) | 0.001 | 0.20 | −0.180 | 0.181 |
| Total oil (%) | Wild bees (WB) | −0.048 | 0.29 | −0.180 | 0.084 |
| | Honeybees (HB) | – | – | – | – |
| | Crop diversity (ERGp) | **1.132** | **1.00** | **0.974** | **1.291** |
| | Mean field size (MFS) | **−0.384** | **1.00** | **−0.500** | **−0.267** |
| | Seminatural habitats (SNH) | **1.079** | **1.00** | **0.882** | **1.277** |
| | Within-field position (edge vs centre) | **−0.070** | **1.00** | **−0.105** | **−0.035** |
| Total tocopherols | Wild bees (WB) | 0.021 | 0.24 | −0.067 | 0.109 |
| | Honeybees (HB) | **0.110** | **1.00** | **0.043** | **0.177** |
| | Crop diversity (ERGp) | 0.049 | 0.30 | −0.049 | 0.148 |
| | Mean field size (MFS) | **−0.803** | **1.00** | **−0.879** | **−0.727** |
| | Seminatural habitats (SNH) | **−0.244** | **1.00** | **−0.355** | **−0.133** |
| | Within-field position (edge vs centre) | **0.025** | **0.88** | **0.002** | **0.047** |
| α-Tocopherol | Wild bees (WB) | −0.017 | 0.24 | −0.133 | 0.099 |
| | Honeybees (HB) | **0.121** | **1.00** | **0.031** | **0.211** |
| | Crop diversity (ERGp) | 0.002 | 0.24 | −0.112 | 0.115 |
| | Mean field size (MFS) | **−0.617** | **1.00** | **−0.719** | **−0.515** |
| | Seminatural habitats (SNH) | −0.040 | 0.26 | −0.180 | 0.100 |
| | Within-field position (edge vs centre) | **0.101** | **1.00** | **0.070** | **0.132** |
| γ-Tocopherol | Wild bees (WB) | **0.104** | **0.56** | **−0.008** | **0.215** |
| | Honeybees (HB) | 0.037 | 0.14 | −0.047 | 0.121 |

(*continued on next page*)

**Table 2** (*continued*)

| Quantity parameters | | Estimate | $\Sigma w_i$ | CI | |
|---|---|---|---|---|---|
| | | | | Lower | Upper |
| | Crop diversity (ERGp) | **0.142** | **0.77** | **0.010** | **0.274** |
| | Mean field size (MFS) | **−0.799** | **1.00** | **−0.910** | **−0.689** |
| | Seminatural habitats (SNH) | **−0.427** | **1.00** | **−0.589** | **−0.265** |
| | Within-field position (edge vs centre) | **−0.118** | **1.00** | **−0.146** | **−0.089** |
| Chlorophylls | Wild bees (WB) | −0.010 | 0.21 | −0.144 | 0.124 |
| | Honeybees (HB) | **−0.161** | **1.00** | **−0.264** | **−0.058** |
| | Crop diversity (ERGp) | **−0.322** | **1.00** | **−0.453** | **−0.191** |
| | Mean field size (MFS) | **−0.189** | **1.00** | **−0.296** | **−0.081** |
| | Seminatural habitats (SNH) | 0.086 | 0.30 | −0.089 | 0.260 |
| | Within-field position (edge vs centre) | −0.014 | 0.27 | −0.050 | 0.021 |
| Carotenoids | Wild bees (WB) | 0.061 | 0.33 | −0.062 | 0.185 |
| | Honeybees (HB) | 0.067 | 0.47 | −0.027 | 0.162 |
| | Crop diversity (ERGp) | **−0.468** | **1.00** | **−0.605** | **−0.331** |
| | Mean field size (MFS) | **−0.109** | **0.80** | **−0.211** | **−0.006** |
| | Seminatural habitats (SNH) | **−0.482** | **1.00** | **−0.644** | **−0.320** |
| | Within-field position (edge vs centre) | 0.016 | 0.30 | −0.0151 | 0.047 |

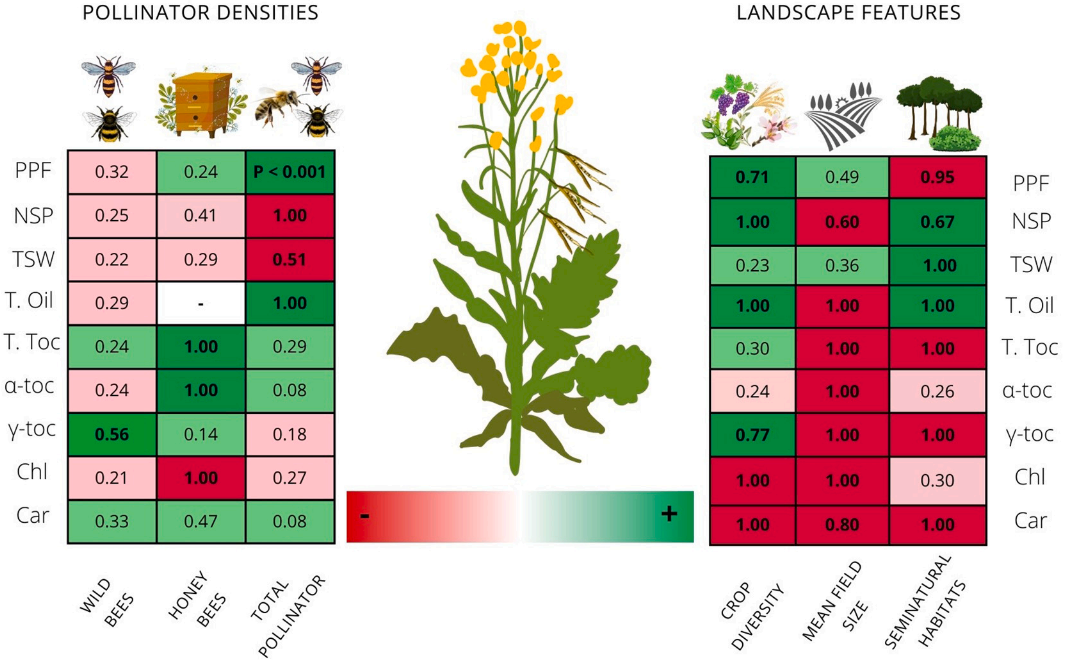
average model that did not contain the variable HB. Both ERGp ($\Sigma w_i = 1.00$) and SNH ($\Sigma w_i = 1.00$) had a positive effect on oil content, whereas MFS ($\Sigma w_i = 1.00$) had a negative effect. Consequently, the oil content in OSR seeds was higher in landscapes with more ERGp and SNH and in agricultural landscapes with smaller field sizes. Conversely, the oil content was lower in edge plants ($\Sigma w_i = 1.00$).

The average model for the total tocopherols obtained from seeds of the OP treatment (Table 2) indicated a positive response to the HB densities ($\Sigma w_i = 1.00$) and within-field position, being higher in edge ($\Sigma w_i = 0.88$). In contrast, total tocopherols decreased in landscapes with a higher proportion of SNH ($\Sigma w_i = 1.00$) and with larger field sizes ($\Sigma w_i = 1.00$). The remaining variables had a relatively minor impact on the overall outcome; however, their effects were not entirely clear.

The average model for α-tocopherol indicated that the HB density, in addition to MFS and within-field position, were the variables with the greatest relative importance ($\Sigma w_i = 1.00$). Only MFS had a negative effect. All three variables were supported by the confidence intervals. The model indicated that seeds grown on the field's edge and in landscapes with smaller field sizes exhibited a higher α-tocopherol content, as well as in the presence of a higher HB density (Table 2). The average model for γ-tocopherol explained that all landscape variables had a high relative importance and were supported by their confidence intervals. The WB density ($\Sigma w_i = 0.56$) demonstrated a positive and clear effect despite containing zero in its confidence interval. The MFS, SNH, and within-field position had negative effects. This model indicated that γ-tocopherol decreased in landscapes with a higher proportion of SNH and in plants from the edge of the field. However, it increased in landscapes with smaller fields and a higher WB density (Table 2).

The pigments present in the seeds varied with all the studied variables. According to the average model, the HB density, ERGp, and MFS variables showed the highest relative importance ($\Sigma w_i = 1.00$) and were supported by their respective confidence intervals. Moreover, they all had a negative effect on total chlorophylls content. The remaining variables had a lower relative importance and less clear effects. The model indicated that the chlorophylls content was diluted in landscapes with higher HB density, lower crop diversity, and larger fields.

Finally, the average model indicated that agricultural landscape variables (ERGp, MFS, and SNH) had the highest relative importance (Table 2) and influenced the reduction in the total carotenoids content in OP treatment seeds. This trend was supported by the respective confidence intervals. HB ($\Sigma w_i = 0.47$) densities positively impacted carotenoids with a clear effect even though its confidence interval contained zero. Consequently, the model indicated that the carotenoids content in



| | WILD BEES | HONEY BEES | TOTAL POLLINATOR |
|---|---|---|---|
| PPF | 0.32 | 0.24 | **P < 0.001** |
| NSP | 0.25 | 0.41 | **1.00** |
| TSW | 0.22 | 0.29 | **0.51** |
| T. Oil | 0.29 | - | **1.00** |
| T. Toc | 0.24 | **1.00** | 0.29 |
| α-toc | 0.24 | **1.00** | 0.08 |
| γ-toc | **0.56** | 0.14 | 0.18 |
| Chl | 0.21 | **1.00** | 0.27 |
| Car | 0.33 | 0.47 | 0.08 |

| | CROP DIVERSITY | MEAN FIELD SIZE | SEMINATURAL HABITATS |
|---|---|---|---|
| PPF | **0.71** | 0.49 | **0.95** |
| NSP | **1.00** | **0.60** | **0.67** |
| TSW | 0.23 | 0.36 | **1.00** |
| T. Oil | **1.00** | **1.00** | **1.00** |
| T. Toc | 0.30 | **1.00** | **1.00** |
| α-toc | 0.24 | **1.00** | 0.26 |
| γ-toc | **0.77** | **1.00** | **1.00** |
| Chl | **1.00** | **1.00** | 0.30 |
| Car | **1.00** | **0.80** | **1.00** |

**Fig. 5.** Summary of the influence of different pollinator densities and agricultural landscape features on seed quantity parameters, pod per flower (PPF), number of seeds per pod (NSP), thousand seed weight (TSW) and seed quality parameters, oil content (T.Oil), total tocopherols (T.toc), α-tocopherol (α-toc), γ-tocopherol (γ-toc), chlorophyll (Chl) a + b, and carotenoids (Car). Bold numbers indicate relevant variables.

OSR seeds was higher in landscapes with smaller field sizes and higher HB density, whereas it decreased in landscapes with greater crop diversity and a higher SNH proportion.

## 4. Discussion

The key finding of this study is the identification of relationships and influences among different characteristics of the agricultural landscape, with a specific emphasis on crop diversity and pollinator densities and their impact on agronomic parameters (quantity/quality) in OSR. This study highlights the fact that WB density increases in agricultural landscapes with greater crop diversity. Moreover, landscapes characterised by higher crop diversity are associated with improved quantity and improvements in OSR seed quality. These findings confirm our first two hypotheses, and in part the third, because WB does not play an important role individually in the quantity and quality of OSR seeds.

### *4.1. Landscape characteristics influence WB density*

Our findings revealed a positive correlation between WB density in rapeseed fields and landscape crop diversity, and a negative correlation with the mean field size. These trends align with those of previous research, indicating that higher crop diversity benefits WB abundance (Aguilera et al., 2020; Sirami et al., 2019). In productive landscapes, diverse crops create temporal variations in habitats and resources, supporting larger bee populations (Cavigliasso et al., 2022; Neira et al., 2024; Raderschall et al., 2021).

In contrast, an inverse correlation has been documented between wild pollinator density and mean field size. Martin et al. (2019) reported that there were 70 % more pollinators in small fields. Small fields with more margins improve landscape connectivity, making it easier for pollinators to move around (Hass et al., 2018a, 2018b; Sutherland et al., 2001). In addition, WBs typically require natural areas for nest or colony establishment and adapt by utilising disturbed or less dense areas compared to forest such as field margins (Hellwig et al., 2022; Rollin et al., 2013). Therefore, the outer part of the crop edge borders with diverse neighbouring microhabitats provide resources for many insects that are favourable for the establishment, growth, and diversification of WB populations in agroecosystems (Bartholomée et al., 2020; Coutinho et al., 2021; Morrison et al., 2017). This could explain the higher abundance of bees observed on the field edges than in the centre.

### *4.2. Influence of pollinator density and pollinator exclusion on seed quantity and quality*

Our study highlights that insect visitation plays a crucial role in OSR yields. The deposition of pollen, facilitated by insect visits, had a positive influence on the flower ratio, and the interaction between open OSR plants and total pollinator density produced a joint effect, increasing PPF while decreasing NSP and TSW. Individually the different groups density of pollinators (WB-HB) did not explain the pollination effectiveness parameters like reported in other studies (Beyer et al., 2021). Pollinators only improve effectiveness in a total way, not individually (Bartomeus et al., 2014; Jauker et al., 2012). Nevertheless, our results underscore the indispensable role of pollinators in maximising yield in OSR crops, consistent with the findings of other authors (Bommarco et al., 2012; Klein et al., 2007) and with more recent studies indicating that HBs and wild insects contribute similar amounts to crop yields (Reilly et al., 2024).

Most quality components of OSR seeds were affected by both the exclusion of pollinators and pollinator density, albeit at different intensities. Plants that interact with pollinators exhibit higher oil content, underscoring the importance of insect pollination in the development of OSR seed oil content (Bartomeus et al., 2014; Perrot et al., 2024). The relationship between oil content and pollinators remains under-researched, yet its importance to market value is significant (Bommarco et al., 2012; Marini et al., 2015). It is likely that this is due to an increase in hybrid vigour, as only a small amount of exogenous pollen is needed to increase the productive parameters of OSR (Lankinen et al., 2018). The total tocopherol content in the rapeseed crop was within the usual range, as reported by Flakelar et al. (2015). However, total tocopherols were not affected by pollination treatment or the density of total pollinators on open inflorescences, but increased with the closeness of the edge and with increasing HB density. The α- and γ-tocopherol concentrations exhibited distinct responses to the pollination treatment. Specifically, γ-tocopherol increased in seeds from inflorescences accessible to pollinators. The observed pattern may be attributed to chlorophyll degradation, which triggers the recycling of phytol into an alternative metabolic pathway for vitamin E biosynthesis (Muñoz et al., 2024). The accumulation of γ-tocopherol suggests that seeds from inflorescences accessible to pollinators have initiated the maturation process and are in a more advanced stage of development. This increased chlorophyll degradation leads to higher production of γ-tocopherol, the form of vitamin E that tends to accumulate in seeds (Munné-Bosch and Falk, 2004).

Higher HB densities were associated with an increase in α-tocopherol, whereas WB density correlated with an increase in γ-tocopherol. The higher concentration of γ-tocopherol in seeds from insect-pollinated inflorescences may be linked to an enhanced maturation process, resulting in the production of more mature seeds in inflorescences accessible to pollinators. This relationship may also be associated with the fact that a higher WB density increases γ-tocopherol, contributing to seeds with greater maturation, as WBs are considered more effective pollinators than HBs owing to a higher likelihood of contact with the flower stigma (Woodcock et al., 2013).

HB density significantly reduced chlorophyll content in insect-pollinated plants. This indicates that a higher density of these pollinators has a direct impact on pigment content. Analysis of the pollinator exclusion experiment demonstrated that insect pollination plays a crucial role in enhancing both the quantitative and qualitative parameters of rapeseed production. Pigments found in OSR seeds were more abundant in plants without pollinators than in OP plants, suggesting that insect pollination influenced pigment concentrations. All pollinator densities, specifically HB densities, were associated with lower chlorophyll levels. Insect pollination expedites fruit and seed ripening, which causes greater decomposition of chlorophylls (Smolikova and Medvedev, 2016). The pattern of chlorophylls in seeds is opposite to that of α -tocopherol, possibly because both compounds have a common precursor (Mène-Saffrané, 2018). This response could be explained because HB are the most abundant group of pollinators in the fields studied. HB collect pollen with high flower constancy, which can be linked to improved pollination efficiency (Montgomery, 2009). Lower concentrations of chlorophyll and higher concentrations of carotenoid are indicators of higher oil quality (Flakelar et al., 2015; Hannoufa et al., 2014). Therefore, based on our findings, insect pollination to enhances oil quality.

### *4.3. The quantity and quality of OSR seeds are affected by the agricultural features of landscape*

The characteristics of the agricultural landscape influence the quantity and quality of rapeseed seeds. Crop diversity was positively correlated with PPF and increased the number of seeds per pod. In contrast, semi-natural areas are particularly important for augmenting the TSW, but they are associated with fewer pods per flower. Rapeseed seed quality was also responsive to diverse landscape features, with specific effects varying depending on the parameters considered.

Crop diversity is a pivotal characteristic of agricultural landscapes that positively affects pollination effectiveness and seed quality. Furthermore, it plays a role in increasing the oil content and γ-tocopherol, while concurrently reducing the presence of pigments in seeds. These patterns are consistent with the findings of previous studies. The positive effect of crop diversity is attributed to its ability to enhance pollinator diversity, leading to increased pollination services for crops (Dainese et al., 2019). Notably, both WBs and HBs have been associated with higher fruit set, elevated oil content, and reduced chlorophyll levels (Bartomeus et al., 2014; Bommarco et al., 2012; Garibaldi et al., 2013). In this study, we could not find a relationship between the crop diversity of the landscape and the improvement in OSR parameters mediated by WBs, but this is not the first report of landscape characteristics affecting both production and phytochemical processes (Magrach et al., 2023; Pioltelli et al., 2024a, 2024b), which is an interesting and novel aspect that requires further investigation.

The observed positive response may be attributed to the correlation between crop diversity in the landscape and WBs. WB density, in conjunction with the contribution of HBs, influences some quantity and quality parameters. HBs showed no relationship with landscape characteristics in the localities (Fig. S1); instead, WBs made the difference in the total pollinator density, a group that is directly related to crop diversity, as indicated above. Our study is the first to show connections between landscapes with diverse crops, pollinator density, and an increase in γ-tocopherol and total tocopherols in seeds. Having various crops in an area appears to create a better environment for OSR production.

Our data indicate that agricultural landscapes with smaller field sizes correlate with an improved number of seeds per pod and generally with better seed quality. Smaller fields may be associated with higher OSR crop yield and plant reproduction (Hass et al., 2018a, 2018b; Magrach et al., 2023). Semi-natural areas positively affect the number of seeds per pod and the weight of a thousand seeds. This is consistent with other studies indicating that oil content in seeds increases with the number of seeds per pod (Vera et al., 2007). Mazzei et al. (2021) underscored the pivotal role of forest fragments in close proximity to OSR fields and their substantial influence on seed production parameters. This highlights the significance of semi natural habitats and their proximity, as emphasised by Halinski et al. (2020, 2018).

## 5. Conclusions

This novel study provides nuanced exploration, unveiling new insights into the agricultural landscape and the quantity and quality of rapeseed crop yield. Our findings underscore the pivotal role of crop diversity through its positive influence on WBs and the enhancement of both seed quantity and quality in OSR crops. In addition, there were positive effects of a greater proportion of semi-natural areas for quantity parameters and smaller fields for quality parameters.

Our investigation of pollination effectiveness revealed a complementary relationship between WBs and HBs. Both groups of bees have a joint effect by increasing the percentage of oil in seeds. Besides, Notably, WBs are linked to seeds that exhibit increased maturity profiles compared with those associated with HBs. This study emphasises the implications of the presence of WBs for seed maturity.

Although this study contributes novel perspectives, our research also underscores the necessity for further enquiries into the intricate dynamics between landscapes, bees, and cultivation practices.

In a broader context, our findings advocate for prioritising the preservation and augmentation of agricultural landscape heterogeneity in the design of agricultural eco-schemes. This underscores the role of agricultural landscape management in supporting WBs and high-quality crop production, presenting a win-win scenario for both biodiversity and agricultural communities.

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## CRediT authorship contribution statement

**P. Neira:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Morales:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **S. Munné-Bosch:** Writing – review & editing, Supervision, Methodology. **J.M. Blanco-Moreno:** Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **F.X. Sans:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

The authors used *ChatGPT* to improve readability and language usage during the writing of this paper. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

## Declaration of competing interest

The authors declare no competing financial interests or personal relationships that may have influenced the work reported in this study.

## Data availability

Data will be made available upon reasonable request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175062.

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