RESEARCH ARTICLE



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Environmentally friendly landscape management improves oilseed rape yields by increasing pollinators and reducing pests

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Abstract

- 1. Pollination and pest control are two major ecological functions sustaining crop yield. In insect-pollinated crops, previous studies have revealed that an increase in resources and habitats in landscapes can increase pest control by natural enemies as well as insect pollination by pollinators. However, data have been lacking that simultaneously considers the effects of landscape on both pollinators and pests, and the direct and indirect effects on yields of farming practices interacting with landscape, bees and pests.
- 2. This study aimed to fill this gap by focusing on oilseed rape (OSR), an insectpollinated crop of high economic value. We first quantified the effects of landscape and farming practices on both bee and pest abundance caught in OSR blooming season in 124 farmed fields over a 6-year study (~20 fields sampled per year), and then used structural equation modelling to assess the direct and indirect links between bees, pests, farming practices and landscape on yield.
- 3. The results showed that landscape had a stronger effect on bee and pest abundance than agrochemical farming practices. Bees and pests decreased with the amount of OSR in the landscape surrounding the focal field, and showed contrasted effects with the amount of meadow and organic farming: positive for bees and negative for pests. Bee abundance also increased with the amount of sunflower in the landscape the preceding year, and decreased with increasing field size.
- 4. While agrochemicals surprisingly had barely any effect on bees and pests, their use improved OSR yield, although at a similar magnitude as bee and pest abundances.
- 5. Synthesis and application. This study, conducted in commercial crop fields, underlines the important contribution of sustainable landscape management for enhancing OSR yield. Despite agrochemicals' ability to improve or maintain OSR yields, their unconditional use is unsustainable due to negative externalities. Therefore, alternative options such as those highlighted in our study—such as reducing field size, increasing the amount of organic farming in the landscape, or sowing OSR in landscapes rich in sunflowers the preceding year-appear to

be relevant tools to promote ecosystem services, maintain yield and conserve biodiversity. These findings support the potential of nature-based solutions to foster more sustainable agriculture.

KEYWORDS

agroecology, fertilizer, flea beetle, honeybee, Lasioglossum, nature-based solutions, pesticide,

1 | INTRODUCTION

Improving agricultural sustainability has become a pressing concern, simultaneously requiring better use of natural resources, lower chemical inputs and increased benefits of biodiversity-related ecosystem services for agricultural production, while ensuring food security (Bommarco et al., 2013; Godfray et al., 2010). However, taken together, the recent decline of insect pollinator populations, increased pest pressure due to climate change, in addition to increase in pollinator-dependent crops areas, may threaten food security (Aizen et al., 2019; Deutsch et al., 2018). Pollinators may contribute up to 35% of crop production (Klein et al., 2007), while pests can reduce overall yield by 20%–30% (Savary et al., 2019). In addition, beneficial effects of pollinators on yield increase with decreasing pest abundance (Sutter & Albrecht, 2016; Tamburini et al., 2019).

Both pollinators and insect pests depend on farming practices and landscape arrangements. Thus, simultaneously managing pests and pollinators may be critical to improve agricultural sustainability (Egan et al., 2020). However, the combined effects of farming practices and landscape on these organisms are rarely considered simultaneously (Egan et al., 2020), making it unknown, for instance, whether pollinators and pests positively react to identical farming practices and landscape features, and which of the latter maximize yields or benefits.

There is clear evidence that pollinators benefit from semi-natural habitats (SNHs) such as grassland or forest, which provide food, shelter and nesting sites (Holland et al., 2017). The stability of floral resources over the season, through organic farming or continuity between early and late mass-flowering crops, is also essential (Grab et al., 2017; Holzschuh et al., 2008). However, high amounts of massflowering crops in the surrounding landscape can also dilute pollinators, resulting in their lower abundance at field scale (Holzschuh et al., 2016). This dilution effect has also been observed for pests (Veres et al., 2013). Pest abundance may also be lower in fields surrounded by SNH or organic farming, mainly because of higher predation rates by natural enemies (Muneret et al., 2019) although the effect of SNH on pest abundance is highly inconsistent between studies (Karp et al., 2018). At field scale, farming practices also modify both pollinator and pest abundance. Pesticides can reduce pollinator abundance (Otieno et al., 2011; Woodcock, Isaac, et al., 2016), as does larger field size, due to limited pollinator dispersion (Hass et al., 2018). Conversely, fertilizer intensity improves plant growth

or nectar quality, which may increase crop attractiveness to pollinators (Otieno et al., 2011). Similar effects, that is, negative for pesticides and positive for fertilizers, have been observed for pests (Otieno et al., 2011), except for field size: that is, pest abundance increases with field size because of the limited dispersion capacity of natural enemies (Haan et al., 2020). Thus, farming practices may have both synergistic and antagonistic effects on pest and pollinator abundance, as well as on yields. In addition, farming practices interact with landscape composition to ultimately shape biodiversity, for example, the effect of SNH on pollinator or pest abundance is more pronounced when pesticide use is low (Gagic, Hulthen, et al., 2019; Park et al., 2015).

This study sought to investigate the complex interplay between landscape features and farming practices and their effects on both pollinators and pests, and how these effects translate into yield in winter oilseed rape fields (see Figure 1), an early mass-flowering crop and main oilseed crops in European Union (OSR, Brassica napus L.). Our study was carried out in 124 OSR fields that were studied over 6 years in southwestern France. This crop is strongly dependent on pollinators, which can increase yield by up to 30% (Bartomeus et al., 2014; Perrot et al., 2018; Woodcock, Bullock, et al., 2016), as well as strongly affected by pests, which may decrease yield by 10%-70% (Rusch et al., 2013; Skellern & Cook, 2018). Pests and pollinators of OSR may further interact, partly depending on farming practices. Both pests and pesticide use reduce the beneficial effect of pollinators on OSR yield (Catarino et al., 2019; Sutter & Albrecht, 2016), while the amount of nitrogen input either compensates for the absence of pollinators or has a synergistic effect with pollinators on yield (Tamburini et al., 2019). Farmers have therefore two means of leverage available to improve OSR yield: landscape management (here, a sort of ecological intensification) to modify pest and bee abundance; or farming practices (agricultural intensification) to increase soil fertility and reduce pest damage, although with, presumably, a negative effect on bees (Figure 1). Synergistic and/or antagonistic relationships between these options and their direct and indirect effects are therefore complex, and remain at best little documented in the case of OSR.

To address this knowledge gap, the first aim of this study was to characterize the effects of landscape features on wild bees and honeybees, that is, the main OSR pollinators in our study site (Perrot et al., 2018), and on pest abundance (Figure 1a) using a recent method without any prior assumption on the spatial scales

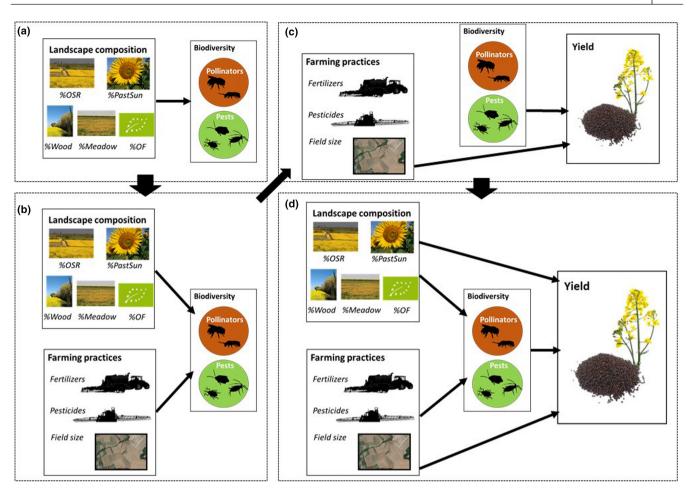


FIGURE 1 Schematic representation of our research strategy to assess the direct and indirect effects of landscapes, farming practices, bees and pests on OSR yields. We first investigated the effect of landscape on bee and pest abundance (a), and then included the effect of farming practices and their interaction with landscape (b). Then we explored the direct effects of bee and pest abundance as well as farming practices on OSR yield (c). Linear models were used for these three steps. Finally (d), using structural equation modelling, we clarify the pathways through which landscape and farming practices affected OSR yields, that is, whether the effect was direct, indirect or both direct and indirect through bee and pest abundances. %OSR, %PastSun and %OF for respectively %oilseed rape, %past sunflower and % organically farmed fields.

of influence of landscape variables (Carpentier & Martin, 2021). We predicted a positive effect of SNH on pollinators and a negative effect on pests (Bartomeus et al., 2014; Woodcock, Bullock, et al., 2016). We also predicted a positive effect of the amount of late mass-flowering crops in the previous year (here, sunflowers) on bee abundance (Häussler et al., 2017) and a dilution effect of OSR on both bees and pests when a high amount of OSR surrounds the focal field (Holzschuh et al., 2016; Zaller et al., 2008). Second, we considered how farming practices interact with landscape features to affect bees and pests (Figure 1b). We predicted that high fertilizer use would increase their abundance, while pesticide use would decrease it, possibly suppressing the beneficial effects of landscape features (Gagic, Marcora, & Howie, 2019; Park et al., 2015). We also expected that field size would decrease bee abundance, but increase pest abundance. Using structural equation modelling (SEM), we finally analysed the combined effects of landscape and farming practices on OSR yield through their direct and indirect effects (Figure 1c,d).

2 | MATERIALS AND METHODS

2.1 | Study site and field selection

The study was carried out in the 'Zone Atelier Plaine & Val de Sèvre', a long-term social–ecological research (LTSER) site of $435\,\mathrm{km}^2$ (Bretagnolle et al., 2018) located in western France. Between 2013 and 2018, we surveyed 124 fields (2013 = 10 fields, 2014 = 22, 2015 = 25, 2016 = 29, 2017 = 18 and 2018 = 20) at this site. Only winter OSR, the main OSR crops in Western Europe, is grown here. This crop blooms between mid-March and the end of May, representing around 8% of the LTSER agricultural area. The OSR sown consists mainly of hybrid varieties (Catarino et al., 2019; Perrot et al., 2018). The focal fields were selected using a moving window procedure (Bretagnolle et al., 2018) to avoid any strong correlation between the three landscape features of interest, that is, those known to be strong drivers of farmland biodiversity: wood habitats (hedges and forest patches), meadows (including temporary grasslands such as alfalfa) and organically farmed fields.

Land use is mapped annually for each of the 13,000 fields in the LTSER, and all information is stored on a GIS database (Bretagnolle et al., 2018). Once OSR fields were selected, we asked farmers for the permission to fieldwork—we obtained this permission in all the fields in which we collected data. Field sizes ranged from 0.84 to 28.49 ha (mean 6.8 ha) and distance between monitored fields were on average 2.3 km (0.24–11.3 km). We used the IGCS soil map (https://www.geoportail.gouv.fr/) to categorize soil types, which belong to four main classes in the LTSER: three are calcareous soils, but vary in soil depth from $20\,\mathrm{cm}$ (n=60), $30\,\mathrm{cm}$ (n=41) to $40\,\mathrm{cm}$ (n=7), and the last is red silt over limestone (n=16). All fields were farmed using conventional agriculture methods and were never sampled in two consecutive years.

2.2 | Landscape metrics

We used landscape data from the year during which pollinators and pests were surveyed in OSR fields to compute the proportion of oilseed rape in the landscape (i.e. area of OSR in the buffer zone minus the area of the focal field; %OSR), the proportion of organically farmed arable fields (%OF), and the proportion of semi-natural habitat within the selected buffer zone. We divided SNH into wood habitats (%Wood) and meadows (%Meadow), as these two habitats can differently affect insect presence (Veres et al., 2013). The proportion of hedgerows was not considered because of its high correlation with the proportion of meadows (Figure S2). We also measured the effect of mass-flowering crops in the surrounding landscape the preceding year by calculating the proportion of sunflowers in the landscape at year n-1 (%PastSun). Sunflowers flower between late June and mid-August and represent 10.4% of the LTSER agricultural area. Sunflower spatial distribution was quite stable between years (yearto-year Pearson correlation at a 2-km radius was 0.75, N = 124). Except between meadows and hedgerows, the landscape metrics showed very low between-class correlation ($r \le 0.5$, see Figure S2).

2.3 | Farming practices

Data on yield and farming practices were collected each year during interviews conducted with farmers after the harvest. We focused on the three main fertilizers (i.e. nitrogen, phosphorus and potassium) to estimate fertilizer intensity in order to assess fertilizer effect on crop attractiveness for bees and pests (Otieno et al., 2011). The amount of inorganic nitrogen used was directly calculated from the fertilizer composition and the quantity applied, while the quantity of nitrogen mineralized from organic fertilizers was deduced using the method described in Jeuffroy and Recous (1999). Pesticide pressure was assessed using the treatment frequency index (TFI; Organisation for Economic Cooperation and Development, 2001). This standard quantitative index allows pesticide-use intensity between fields to be compared, as TFI measures the intensity of applications as the dosage applied per unit of cultivated area in relation to the recommended dosage per crop type as provided under national guidelines

(Organisation for Economic Cooperation and Development, 2001). Farming practices are summarized in Table S4. Pesticide-use intensity was the sum of the TFI of insecticides, herbicides and fungicides, and fertilizer-use intensity was the sum of nitrogen, phosphorus and potassium, all centred and scaled before being summed (Jorgenson & Kuykendall, 2008). Fertilizer and pesticide intensities were not related to soil types (ANOVAs, all p > 0.1).

2.4 | Insect sampling

Insects were sampled during the OSR flowering period, from Julian day 90 (1 April) to 170 (20 June; Perrot et al., 2018). Three complementary methods were used to assess insect abundance: pitfall traps, pantraps and sweep netting along transects. The pantrap method is appropriate for estimating wild bee abundance (especially for the Halictidae family, such as Lasioglossum spp; Perrot et al., 2018) and pest abundance, at least for species found on plant inflorescence (Lundin et al., 2012). Honeybee abundance is better estimated by sweep netting (Perrot et al., 2018; Westphal et al., 2008). Pitfall traps were used to estimate ground pest abundance, for example, flea beetles (Coleoptera: Alticini, Lundin, 2019). Pantraps consisted of bowls of three different colours and were set at the canopy of OSR plants. Pitfall traps were put on ground. Four to five pitfalls and 12 to three pantraps were set per field according to year at two different positions in the field, that is, the edge and centre (~50m from edge) of fields. Both pantraps and pitfalls were filled by soap water and left in fields during 4 days. Sweep netting consisted, in each field, in two or three transects of 50m according to year. See Appendix A for the complete catch protocol description, the catch summary and correlation between catches. For bees, we considered the two dominant OSR pollinators in our samples, that is, genus Lasioglossum spp. (a wild bee genus, 51.2% of total bee sampled) and honeybees (88.1%) respectively for pantraps and sweep netting (Table S1; Catarino et al., 2019; Perrot et al., 2018). These two genera were also the main contributor of OSR pollination in our study site (Perrot et al., 2018). Concerning pests, we considered four categories regarded as responsible for most damage in OSR crop production (Lundin, 2019; Lundin et al., 2013; Rusch et al., 2013; Sutter & Albrecht, 2016; Zaller et al., 2008): aphids (Aphididae spp.), flea beetles (Alticini spp.), weevils (Curculionidae spp.) and pollen beetles (Meligethes spp.). Pest abundance estimated by the two methods was not correlated (r = 0.06, see Figure S1). Different species were generally caught per method type: pantrap catches mainly consisted of pollen beetles (57%) and aphids (21.9%), while pitfall catches mainly consisted of flea beetles (56.7%) and pest weevils (34.5%, Table S1).

2.5 | Statistical analyses

First, we used linear models (LMs) to analyse landscape effects on bee and pest abundance in OSR fields (Figure 1a). Landscape effects were investigated either on total pest abundance (sum of weevils, flea beetles, aphids and pollen beetles: hereafter, pest abundance) separately

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per method (pantrap or pitfall) or separately on each of the four groups. Similarly, landscape effects were analysed on Lasioglossum and honeybee abundance, separately or combined (hereafter, bee abundance). To sum abundances of Lasioglossum and honeybees obtained with different trapping methods, following Catarino et al. (2019), we centred and scaled Lasioglossum abundance over the 6 years, while honeybees were centred and scaled for 2013-14 and 2015-18 separately to account for changes in count methodology between these two periods. The proportion of OSR (%OSR), woodland (%Wood), meadows (%Meadow) and organic farming (%OF) in the landscape in a given year and the proportion of sunflowers in the landscape in the preceding year (%PastSun) were used as explanatory variables. We did not include past %OSR which was found to have no effect on bee or pest abundance in preliminary analyses. The spatial scale of influence of each landscape metric was determined by maximizing the likelihood of the LM using the 'bsiland' function of the 'SILAND' R package (Carpentier & Martin, 2021). This method allows to estimate simultaneously (but independently) the effect of each landscape variables and their spatial scales of influence. Spatial scale was estimated from 100 m (i.e. the minimum distance to the neighbouring field) to 2,000 m (i.e. higher range of pollinators' dispersion capacity) from the field border (Torné-Noguera et al., 2014). There was a very low overlap between buffers (on average 9.76% ± 9.79 SD on each buffer size estimated with the 'Siland' method), indicating that sample fields remained independent statistically. For the sake of robustness, we however ran LMs using bootstraps for randomly eliminating sampled field with overlapping buffers and found identical results (data not shown).

Next, we investigated the effect of farming practices at field scale and in interaction with landscape features on bee and pest abundance (Figure 1b). We used results of the previous models (i.e. the variables retained as well as the spatial scales of effects) and included three new explanatory variables, all related to farming practices: field size, pesticide intensity and fertilizer intensity. We also included soil type and interactions between pesticide use with each landscape variable. Pesticide use was preferred to insecticide use because herbicides and fungicides were shown to affect insects directly or indirectly (Potts et al., 2016). All analyses were also ran, however, using insecticide use (instead of pesticide use). A backward model selection procedure based on Akaike information criteria (AIC; Burnham & Anderson, 2004) was applied to compare the relative performance of the different combinations of variables.

Next, the relative contribution of farming practices and biodiversity on OSR yield was investigated using a LM with soil type, field size, fertilizer-use and pesticide-use intensity, and bee and pest abundance as explanatory variables (Figure 1c). Interactions between fertilizer and pesticide use with bee and pest abundance were also included to explore their potential synergistic or antagonistic effects (Sutter & Albrecht, 2016; Tamburini et al., 2019). For these analyses, we used pest abundance estimated by pitfall trapping rather than by pantrap, since a higher correlation (negative) between pests and yield was observed with the former (pitfall, r = -0.23, $t_{122} = -2.65$, p = 0.009) than the latter (pantraps, r = 0.006, $t_{122} = 0.07$, p = 0.94). Backward model selection procedures were also used in this analysis. Since OSR yield varies annually and

spatially at a large spatial scale due to pedo-climatic effects (which can be considered as confounding effects), we also conducted this analysis using an estimated OSR yield (explained variable) obtained by correcting observed yield by weather conditions and field spatial coordinates (latitude and longitude of the OSR field). As the results were similar (see Table S6), we only present the results with the uncorrected OSR yield. We did not include OSR cultivars in models because previous analyses in our study site showed an absence of effect of cultivars on the insect pollination benefit to OSR yield (Perrot et al., 2018).

Finally, we built a structural equation model (SEM; Lefcheck, 2016) to clarify the pathways through which landscape and farming practices affected OSR yields, that is, whether the effect was direct, indirect or both direct and indirect through bee and pest abundances. We used linear mixed models with soil depth as a random effect to fit the SEMs. The SEM thus included direct paths to yield from farming practices, landscape features, bee and pest abundance, as well as indirect paths from landscape, soil type and farming practice effects on bee and pest abundance (Figure 1). To avoid overfitting of our models, farming practices and landscape variables that were removed from previous models by stepwise selection were not considered in the SEM model. Landscape was represented by the landscape variables retained in the landscape analysis for bee abundance because this spatial scale was largest than the one for pests and thus included all other landscape metrics. We further ran one different SEM with buffer size estimated for pest abundance but also by using only insecticide, to ensure that this a priori choice did not alter the results. SEM model was also run without field size to test for potential confounding effects between field size and landscape structure. We used a bootstrapping, that is, running 10,000 simulations, to test the probability that the path coefficient differs from zero.

All analyses were performed using R 3.6.2 software (R Core Team, 2015). For all LM models without interaction terms, we checked for spatial autocorrelation in the residuals using a Moran test (Bivand & Wong, 2018). Collinearity between variables was checked with the variance inflation factor (VIF). None spatial autocorrelation (Moran test, all p > 0.06) was found as well as collinearity (all VIF < 1.8). We used the 'SILAND' package to estimate the spatial extent of landscape variables (Carpentier & Martin, 2021), the 'spdep' function for the spatial autocorrelation test (Anselin et al., 2012) and the 'SEMEFF' package for SEM (Murphy, 2021). To meet the assumption of normality and homoscedasticity of model residuals, field size, fertilizer and pesticide intensity, and bee and pest abundance were transformed either as $\log 10(x+1)$ or as $\log 10(x+abs[min]+1)$ when the smallest x-value was <0, and the amount of organically farmed fields, woods and meadows were square-root transformed (Morrissey & Ruxton, 2020).

3 | RESULTS

3.1 | Landscape effects on bees and pests

Using LM with only landscape variables showed that landscape features better predicted bee than pest abundance, with respectively 20%, 10% and 9% of variance (R^2 model) explained for bees, pests

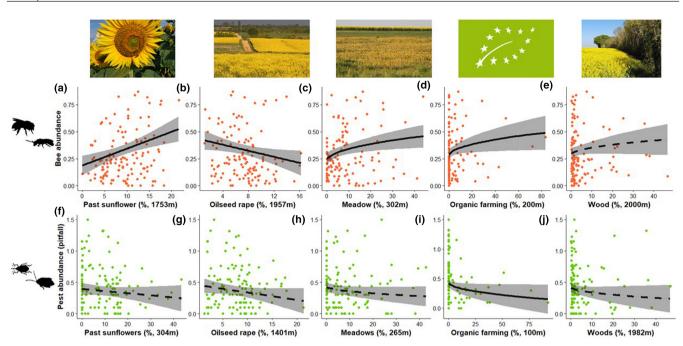


FIGURE 2 Effect of the proportion of (a) past sunflowers, (b) oilseed rape, (c) meadows, (d) organically farmed fields and (e) woods in the surrounding landscape on (a–e) bee and (f–j) pest abundance (estimated by pitfall traps). Solid lines show significant effects and dotted lines non-significant effects as predicted by linear models. Shaded areas show confidence intervals at 95%. Buffer size estimated for each metric using the Siland method is indicated in brackets on the *x*-axis. Bee and pest abundance is log-transformed (see Section 2).

estimated by pantrap and pests estimated by pitfall trap (Figure 2 and Table S2 for summary of linear models). Total bee abundance significantly increased with %PastSun (amount of sunflowers in previous year) at a 1,753 m radius (Figure 2a), as well as with %OF and %Meadow at smaller spatial scales (<350 m from field border, i.e. in neighbouring field; Table S2, Figure 2c-e), and significantly decreased with %OSR at 1957 m (Table S2, Figure 2b). Separating bees between *Lasioglossum* and honeybees showed that both increased significantly with %PastSun, as well as %OF, although only significantly for *Lasioglossum* (Table S3). Honeybees also increased with %Meadow and %Wood, but decreased with %OSR (Table S3).

Pest abundance estimated from pitfall traps decreased significantly with %OF at a 100-m radius outside the focal field (Table S2, Figure 2j), while pest abundance estimated with pantraps decreased with %Meadow at 433 m although not significantly (Table S2). When investigating pest taxa separately, only aphid and pollen beetle abundances (pantraps) decreased with %Wood (Table S3). Weevil abundance (pitfalls) increased significantly with %OSR, but flea beetle abundance (pitfalls) was not affected by landscape (Table S3).

3.2 | Effects of farming practices and landscape on bees and pests

Accounting for both farming practices and landscape effects increased the goodness-of-fits of the models, especially for total bees ($R^2=24\%$ compared to 10% with only farming practices) and pests caught with pitfall traps ($R^2=17\%$, compared to 6% with only farming practices). Bee abundance significantly decreased with increased

field size (Table 1). Neither fertilizer nor pesticide intensity significantly affected bee abundance, and pesticide intensity was actually deleted by the model selection procedure. No significant interactions were detected between landscape and farming practices on bee abundance (Table 1). Similarly, farming practices did not affect pest abundance whatever the pest estimation methods (Table 1). Models were not improved when using the insecticide treatment frequency index (data not shown). Pest abundance estimated with pitfall traps varied with soil quality with higher abundance in superficial (i.e. >20 cm depth) calcareous soils than in other soils (Table 1).

3.3 | Relative contributions of farming practices, bees and pests on yield

Farming practices, bee and pest abundance, soil quality and field size explained 35% of variance in OSR yield, all having a significant effect on yield (Figure 3; see Table S7 for summary of linear model). Yields were on average 20.3% higher in red soils than in calcareous soils, and increased with pesticide and fertilizer intensity, although rapidly saturating (Figure 3a,b). Bee and pest abundance contributed equally but in opposing directions to OSR yield, with a 32.5% (Cl: 15.2%–49.9%, i.e. +0.83 t/ha; Figure 3c, Table S7) increase effect on yield between the lowest and the highest bee abundance. In contrast, yield was 25.4% (Cl: 9.8%–41%; i.e. –0.77 t/ha; Figure 3d, Table S7) higher in fields with the lowest pest abundance compared to those with the highest pest abundance. Fertilizers interacted with both bee and pest abundance in their effects on OSR yield by reducing respectively their positive and negative effect on yield, although with marginal significance (Table S7).

TABLE 1 Summary of the linear model on the effects of farming practices and landscape and their two-way interactions on bee and pest abundance (estimated by pantraps or pitfall traps). Significant effects (p < 0.05) are in bold. Shaded cases represent variables excluded by the model selection procedure. All abundances, field sizes and farming practices are log-transformed. The amount of organic farming, woods and meadows are square-root transformed. The spatial extent of the effect of each landscape variable was estimated using the Siland method.

	Bee abundance			Pest abundance (pantrap)			Pest abundance (pitfall)		
	Buffer (m)	F	р	Buffer (m)	F	р	Buffer (m)	F	р
Soil type								3.134	0.028
Field area		6.021	0.016						
Fertilizer intensity		3.134	0.079						
Pesticide intensity					0.09	0.765		0.113	0.737
Amount of past sunflower	1753	8.704	0.004						
Amount of oilseed rape	1957	4.591	0.034	597	0.657	0.419	1401	3.547	0.062
Amount of organic farming	200	6.904	0.01				100	4.627	0.034
Amount of wood				1973	3.06	0.083			
Amount of meadow	302	6.206	0.014	433	3.816	0.053	265	1.448	0.231
Pesticide intensity × oilseed rape					2.247	0.137			
Pesticide intensity×amount of meadow								4.532	0.035

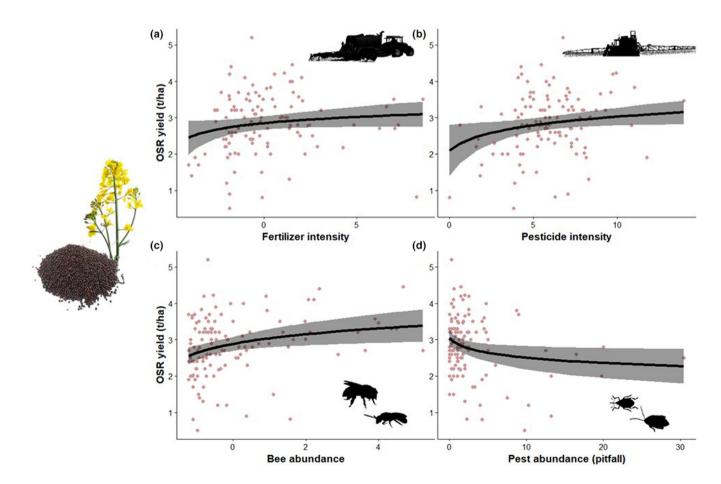


FIGURE 3 Effects of (a) fertilizer intensity, (b) pesticide intensity, (c) bee and (d) pest abundance (estimated by pitfall traps) on OSR yields. Lines show significant effects as predicted by linear models. Solid lines represent significant relationships. Shaded areas show confidence intervals at 95%.

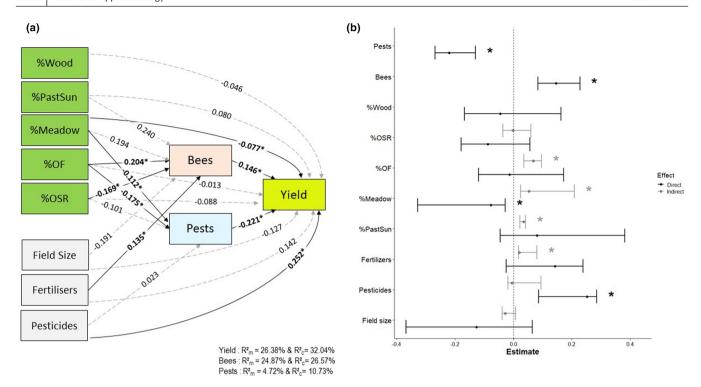


FIGURE 4 (a) Structural equation modelling (SEM) depicting the direct and indirect effects of farming practices and landscape on OSR yield through their effects on bee and pest abundances. Arrows are solid and black when the relationship is significant and dotted and grey when non-significant. The marginal and conditional R^2 (denoted as R^2_m and R^2_c respectively) for yield, bee and pest abundances are provided. (b) Direct and indirect effects of farming practices, field size, landscape, bee or pest abundance on yield. Estimates and their confidence intervals were obtained by bootstrapping. Direct effects are black, and indirect effects are grey. Stars show significant effects. %OSR, PastSun and %OF for respectively %oilseed rape, %past sunflower and % organically farmed fields.

3.4 | Disentangling the effects of landscape, biodiversity and farming practices on OSR yield

Overall, we found that landscape features had indirect effects on OSR yield except %Wood and %OSR which had no effect, either direct or indirect (Figure 4). %OF had a positive indirect significant effect on OSR yield by increasing bees and reducing pests. %PastSun indirectly increased OSR yield by increasing bees, as %Meadow did, by reducing pests. (Figure 4b). The positive effect of %Meadow was, however, buffered by its direct negative relation with OSR yield (Figure 4b). Conversely, farming practices had mainly direct effects on OSR yield when significant effects were detected: pesticide use had a direct positive effect on OSR yield, while fertilizer use direct effect was close to significance, and indirectly increased yield through bees (Figure 4b). Replacing pesticides by insecticides only did not change the general pattern, although insecticides had not significant direct effect on yield (Figure S3). Field size had both negative direct and indirect effects, but non-significant (Figure 4b). In addition, removing field size from the model improved landscape effects overall (Figure S4), suggesting that field size across the study site varied with landscape features (e.g. smaller field sizes in landscapes with many meadows). The structural equation model thus corroborated previous results obtained with LMs, but highlighted the potential for landscape effects to indirectly, through bees and pests, having strong

consequences on OSR yield (Figure 4b). It also confirmed the role of pesticides, having a strong positive effect on OSR yield although this was counterbalanced by a negative and similarly strong effect of pests. Running the SEM with a landscape scale effect estimated for pests revealed a stronger positive indirect effect of %OF but a lower effect of %PastSun on OSR yield (Figure S5).

4 | DISCUSSION

Our results support the growing literature on the effectiveness of ecological functions in maintaining high levels of agricultural productivity while being sustainable (Kleijn et al., 2019). Importantly, our findings reveal that sustainable landscape management of massflowering crops and semi-natural habitat in addition of fields under organic farming can enhance crop yields by improving natural regulation processes such as pollination and natural pest control. The study found that OSR yields were higher in landscapes with a high amount of sunflowers in the preceding cultivation season, presumably hosting higher bee abundance, as well as in landscapes with a high amount of organic farming, leading to reduced pest abundance. The study was novel in considering the influence of key landscape features on bees and pests collected in the same fields, together with the measurement of crop yields. Thus, these results can contribute to paving the way to more sustainable management options.

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4.1 | Landscape features enhance bees and suppress pests

We found that a higher proportion of organic farming and meadows in the landscape increased bee abundance and decreased pest abundance, and showed indirect effects on OSR yields. These findings confirm the key role of these landscape features in providing floral resources and nesting habitats for bees (Holzschuh et al., 2008; Kennedy et al., 2013). While organic farming is widely acknowledged for its capacity to increase pollinators (Holzschuh et al., 2008), its effect on pests is more debated as organically farmed fields can be reservoirs for pests (Muneret et al., 2018). Yet our findings suggest that a higher amount of organic farming in the landscape actually reduces pest pressure, through an increase in natural pest control, as these fields shelter natural pest enemies (Muneret et al., 2018). This phenomenon has also been observed for meadows (Veres et al., 2013). However, contrasting and complex effects of meadows and organic farming were found on bees and pests. For example, while the amount of meadows in the landscape increased honeybee abundance, it had no effect on wild bees (Lasioglossum). This may be because most Lasioglossum do not depend on semi-natural habitats for breeding, since they nest in bare soil (Torné-Noguera et al., 2014).

As predicted, we found a dilution effect on bees related to the amount of OSR in the landscape neighbouring the focal field (Holzschuh et al., 2016). The scale of the spatial effect of OSR on bees was relatively large (i.e. 1,957 m) compared to the scale at which it is generally explored (i.e. 1,000 m; Holzschuh et al., 2016), although this spatial extent was much lower when separately considering honeybee and Lasioglossum abundance (i.e. 609 and 443 m respectively), probably in relation to different dispersal capacities (Torné-Noguera et al., 2014). In contrast to the effect of the percentage of OSR fields, bee abundance strongly increased with the amount of sunflowers in the landscape the preceding year. This positive effect of the presence of late floral resources on pollinators in OSR was predicted in a model by Häussler et al. (2017). To our knowledge, ours is the first empirical study to demonstrate the interannual relationship between a late mass-flowering crop (sunflowers) and an early mass-flowering crop (OSR) on bees. Indeed, landscape with a high amount of sunflower can be attractive for beekeepers resulting in a higher hives density and honeybee abundance. However, the positive effect of sunflowers was also detected for Lasioglossum. Our results therefore extend those of Riedinger et al. (2014), who showed a temporal spillover of bumblebees between oilseed rape and late-flowering sunflower fields within the same year.

4.2 | Farming practices loosely affect bee and pest abundance

We postulated that high fertilizer use would increase bee and pest abundance, while pesticide use would decrease it, possibly

suppressing the beneficial effects of landscape. Rather unexpectedly, we found that farming practices had fairly small effects on bee or pest abundance, and therefore no indirect effects on OSR yields. Pesticide use was not found to affect bees or pests, despite a weak relationship being found in a previous study at this study site with a smaller dataset (Catarino et al., 2019). Park et al. (2015) showed that the time-lag between pesticide application and negative effect on bees can be greater than 1 year and may explain the absence of relation in our study that considers pesticides application of the sampling year. The use of the treatment frequency index may also explain the absence of a negative effect of pesticides on biodiversity, because this quantitative index fails to correctly estimate toxicity (Möhring et al., 2019). However, pesticide use cancelled out the negative effect of meadows on pests, as has been found in previous studies showing that the positive effect of SNH on pest predation was removed by pesticides (Gagic, Hulthen, et al., 2019). This is likely due to the well-known negative effect of pesticides on the community of natural enemies (Greenop et al., 2020). We additionally considered field size as a farming practice in our framework as this depends on farming decisions. We found that increased field size had a negative effect on bee abundance, suggesting that bee diffusion in OSR fields is limited by their flight distance capacity (Torné-Noguera et al., 2014) or bee abundance was diluted in larger fields (Holzschuh et al., 2016).

5 | SYNTHESIS AND MANAGEMENT IMPLICATIONS

Over the past decade, evidence has been accumulating on the ability of nature-based solutions to maintain or increase crop production while preserving the environment and biodiversity (see the review in Kleijn et al., 2019). Our results confirm that ecological functions that enhance natural regulation, such as insect pollination and natural pest control, may be a sustainable pathway to improving OSR yields, hence a way to foster sustainable farming. We found that OSR yields benefited from biodiversity at almost the same magnitude as agrochemical inputs, but biodiversity benefits were indirectly mediated by landscape features, as shown by the SEM analysis. A similar magnitude of effects on yields between bees and agrochemicals has been previously found (Catarino et al., 2019), but our study extended this to pests. Moreover, similar yields in fact means increased margins for farmers, since biodiversity-based solutions avoid costly agrochemical application costs (Catarino et al., 2019). Further studies should, however, be conducted to confirm our results by including pest damage measures and extending pest survey all over the cropping period (from sowing to harvest).

This joint analysis of the effects of biodiversity, agrochemicals and landscape features on OSR yield highlights the significant role of landscapes as a management tool for simultaneously improving bee abundance while reducing pests. Different landscape elements as well as contrasting spatial scales seem to be involved. In particular,

landscapes rich in organic farming and with high amounts of sunflowers may ensure high flower resources and nesting sites for bees and the natural enemies of pests, allowing farmers to increase their yields without increasing pesticide use. This pattern improved when field size was moderate. However, while more ecological landscape management had positive effects on bees and negative effects on pests, this effect was lower than farming practices, suggesting that a combination of reducing agrochemical inputs and field size, in parallel with improving landscape features for bees and pests, may be the best solution to optimize not just yields but other ecosystem services.

AUTHORS' CONTRIBUTIONS

V.B. and S.G. designed the study; T.P. performed the statistical analysis, with help from S.G.; S.G. and T.P. wrote the first draft of the manuscript; All authors contributed substantially to revisions and editing, and gave their final approval for publication.

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CONFLICT OF INTEREST

We declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available via the Zenodo Repository https://doi.org/10.5281/zenodo.6487661 (Perrot et al., 2022).

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