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Crop yield loss under high insecticide regime driven by reduction in natural pest control

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Current agricultural pest management mainly relies on the use of synthetic insecticides with strong adverse impacts on the environment or humans. Decreasing crop productivity in the case of pesticide-use reduction has been a prominent argument against such reductions. However, the relationship between insecticide use and crop yields is complex. Through long-term monitoring of yields, farming practices, pest populations and natural pest control across 383 fields of oilseed rape—one of the most insecticide-intensive crops in Europe—we reveal a negative relationship between yield and insecticide use when application rates exceed 36.2 g ha^{-1} of active ingredients. Our analyses indicate that this negative effect of insecticide use is primarily driven by its adverse impacts on natural pest control, affecting both insect pests and weed seed regulation. This leads to increased pest abundance levels and, consequently, greater yield losses. Our study demonstrates that beyond a certain threshold, insecticides not only impose adverse environmental impacts and additional application costs for farmers, but also negatively affect overall crop production levels. Our results highlight the need for solutions that extend beyond the farm level, since we also demonstrate that landscape elements such as meadow and crop diversity play a crucial role in regulating pest populations.

1. Introduction

Agricultural crop protection is key for food security, with crop losses from pests and diseases estimated to range between 20 and 30% globally [1,2]. Current pest management is dominated by pesticides: while herbicides dominate in tonnage, insecticides come ahead because of their major negative impacts on the environment, human health and essential ecosystem services (e.g. [3–5]). Insecticide reduction is currently put forward by national and international public policies as a consequence of these well-documented negative effects. However, the potential yield loss and threats to food security associated with reduced insecticide use have been the primary arguments against implementing such reduction [6]. Actually, the relationship between insecticide use and crop yield remains poorly documented and the few studies addressing this issue reported inconsistent outcomes: either positive [7,8], neutral [9,10] or even negative effects [11,12].

The interplay between the beneficial and detrimental effects of insecticide use on pest populations and their natural enemies ultimately determines the nature of the relationship between insecticide use and crop yield [11].

Natural pest control provided by predators and parasitoids can reduce insect pest abundance up to 60–70% [13–15]. When promoted by adequate habitat management strategies, natural pest control can be as effective as insecticides in controlling pests, and may even lead to increased crop yield [16,17]. In contrast, insecticide use can reduce natural pest control efficiency by direct lethal impacts on natural enemy communities [8,11,18], or through sub-lethal effects involving behavioural changes [19,20]. For instance, insecticides can reduce natural enemies' ability to move or detect pests [11,21]. These negative side effects of insecticides on natural pest enemies can result in increased pest abundance levels, secondary pest outbreaks [22,23] and higher crop damages [11,12] and in turn greater yield losses. Hence, a positive relationship between insecticide use and crop yield may emerge if the benefits of limiting pest damage through insecticides outweigh the negative side effects on natural enemies. Conversely, negative relationships may occur if the harmful impacts of insecticides on pest natural enemies surpass the pest control provided by insecticides. In addition, a nonlinear relationship may occur if the beneficial effects of insecticide use on pest control services diminish as the negative effects on natural enemies intensify. However, very few studies have addressed these issues, and those that have produced inconsistent results, often with limited sample sizes or short study durations [8,11,12]. Moreover, these studies only focused on single natural pest control–insecticide interactions or relied solely on controlled field experiments, which do not account for variations in farming practices.

In this study, we investigated how insecticide use affects natural pest control of insect pests as well as weeds and, in turn, crop yield in oilseed rape. Oilseed rape is a relevant case study for examining these relationships as it is the most pesticide-intensive arable crop in France [24]. This crop shelters a wide variety of insect pests and weeds [25], while natural pest control plays a critical role in regulating them [26–31]. We used data from 383 oilseed rape fields sampled under real farming conditions in western France from 2011 to 2020; and an analytical framework that integrates the various direct and indirect pathways through which landscape and pesticide use interact in shaping pest and natural enemy abundances and, consequently, crop yield (see figure 1 for a conceptual framework). First, we quantified the total effect of insecticide use on yield, then the relationships between insecticide use, predation rates from natural enemies and abundance levels of pests and weeds (figure 1). Then, using structural equation modelling (SEM), we contrasted direct and indirect pathways that best underlie relationships between insecticide intensity, natural pest control services, insect pest and weed abundance levels and yields (figure 1). All along these analyses, we accounted for landscape features as they may buffer the negative effect of insecticides on natural pest control [7,27,32,33]. We used quadratic terms in our models since we expected nonlinear relationships, especially between the use of insecticide and crop yield at field scale. Indeed, at low levels, insecticide may increase crop yield because the crop would benefit from both natural and insecticide pest control since natural enemies would survive [33,34]. At higher levels, a reduction in the abundance or activity of natural enemies would occur such that only insecticides would be involved in pest control and yield will stabilize or even decrease if insecticide use does not fully replace natural pest control of insects [23]. We predicted the shape of the relationships between insecticide intensity and insect pest abundance to be convex, while the relationship between insecticide intensity and crop yield to be concave (figure 1).

2. Material and methods

(a) Study area 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 km² [35] located in western France. For this study, farming practices and yield were monitored on 383 fields between 2011 and 2020. Insect pests and insect predation rates were assessed in 135 of these fields (2013–2019) while weed abundance and seed predation rates were sampled on 133 fields (2014–2020; see electronic supplementary material, table S1, for number of fields with surveys or monitoring per year). Altogether, both abundance and predation rate of both insects and weeds were measured in 115 fields. Fields were selected randomly, using a moving window procedure [35] to avoid strong correlations between four landscape features known to be strong drivers of natural enemies: crop diversity (estimated by crop Shannon index), percentage of meadows (including temporary grasslands such as alfalfa), percentage of woody habitat (including forest and hedgerow) and percentage of organically farmed fields in 1 km² discs [28]. Land use is mapped annually for each of the 13 000 fields in the LTSER, and all information is stored in a GIS database [35]. Once oilseed rape fields were selected, we obtained permission from farmers to do fieldwork in all fields in which we collected data. Field sizes ranged from 0.2 to 31.5 ha (mean 6.8 ha). We used the IGCS soil map (https://www.geoportail.gouv.fr/) to categorize soil types, which belong to five main classes in the LTSER: three are calcareous soils, but vary in soil depth from 20 cm (n = 170), 30 cm (n = 134) to 40 cm (n = 26), red silt over limestone (n = 47). Other fields (n = 6) belong to soil type categories other than the previous one and were regrouped in the category 'others'. Fields were all farmed using conventional agriculture methods. None were sampled in two consecutive years. The oilseed rape sown in the fields consisted mainly of hybrid varieties.

(b) Estimation of predation rates of pests and weeds

We used sentinel cards to estimate predation rates of two different prey types by their natural enemies [36]: insects (*Acyrthosiphon pisum* [28]) and weed seeds (*Viola arvensis* [28]). Insect and seed sentinel cards were positioned on the ground. On each sentinel card, three aphids or 10 weed seeds were glued with organic glue on the rough side of 5 cm × 6 cm sandpaper cards [36,37]. Cards were frozen at −20°C for 24 h before the experiment to avoid an attractant or deterrent effect on predators from glue evaporation [36].

In each field, we selected two parallel transects of 21 m long and separated by at least 10 m, to ensure independence between transects, and at least *ca* 30 m from the field edge (electronic supplementary material, figure S1). Sentinel cards were, on

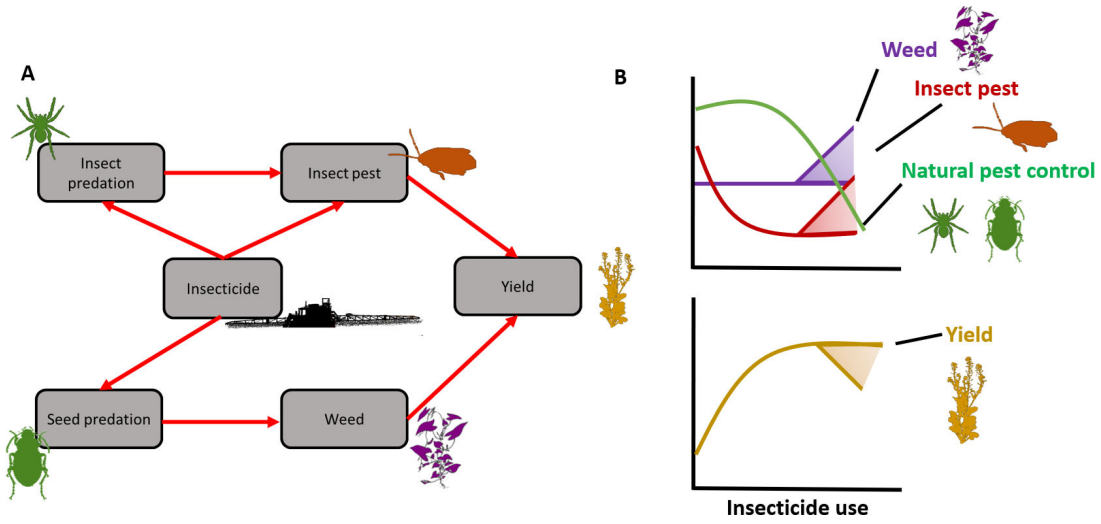

Figure 1. A conceptual framework. (A) Schematic representation of the relationships between insecticide use, natural pest control (insect pest and weed seed), insect pest and weed abundance and yield, with red arrows representing expected negative relationships. (B) Expected relationships between insecticide use and natural pest control, pest/weed abundance and yield. For insect and seed natural pest control, we expected a negative relationship with insecticide at high use (green curve). For insect pest abundance, we expected a saturating relationship between insecticide use and insect pest abundance (solid red curve) as insecticide reduces insect abundance at a minimal level or an increase of insect pest abundance if insecticide use does not totally replace insect pest control (shaded red area). This relation between insecticide use and insect pest abundance will shape the relation between insecticide use and yield that could be either saturating (solid yellow curve) or quadratic with negative effect at high use of insecticide (shaded yellow area). For weed abundance, we expected no relation with insecticide use (solid purple curve) or a positive one at high use of insecticide if insecticide reduces weed natural pest control based on insect herbivores or seed eaters (shaded purple area).

average, set up at 131.1 Julian days (±27.2 s.d.). On each transect, four cards of each prey type (i.e. eight for each prey type per field) were set, each 7 m apart (electronic supplementary material, figure S1). Seed and ground-level aphid cards were placed on the ground in the same position and spaced 40 cm apart (electronic supplementary material, figure S1). Soil cards were folded in half to provide a tent-like shelter and limit deterioration of the glued prey caused by climatic factors (e.g. rain, sun and wind; electronic supplementary material, figure S1). Each field was sampled twice to account for temporal variation of predation rates throughout the season [38] except in 2018–2020 due to high workload. Sessions were spaced at least 48.7 (±12.1 s.d.) days. Predation rates were averaged between the two sessions (for 2014 and 2017) to account for variation in sampling effort among years and avoid replications per field as usually done for these kinds of data [7,28,39].

(c) Insect pest and weed sampling

In the same fields, we estimated insect pest abundance with pitfall traps. Pitfall traps were placed at ground level to estimate ground-level insect pest abundance [40]. Traps were placed during oilseed rape flowering each year. The date for setting the traps differed by 3.9 (±10.1 s.d.) days from setting the sentinel insect cards. In 2014, five pitfall traps were installed per field: two within the first 5 m of the field, one at 25 m and two at 50 m into the field from the edge. In 2015 onwards, the pitfall trap at 25 m was removed to reduce the workload (electronic supplementary material, figure S1). Pitfall sampling was repeated twice a year from 2014 to 2017, whereas only one sampling was performed in 2018 to 2019. Pitfalls were filled with water and left in the field for 4 days. Pest species was determined by a professional entomologist. In each field, we computed pest abundance as the sum of the five most common pest groups found in our study site, i.e. flea beetles, weevils, aphids, leafhoppers and pollen beetles [25,28]. The pest abundance was averaged per field and finally between the two sessions to take account of sampling effort variation between years and avoid replications per field. Thus, only one value per field and per group was available.

Weed abundance was sampled in twenty 1 m² quadrats in each field in the field core. The 20 quadrats were spaced 10 m apart and placed along two transects of ten 1 m² quadrats separated by 40 m and orthogonal to crop rows (electronic supplementary material, figure S1) [28]. Each 1 m² plot was georeferenced and divided into four 0.5 m × 0.5 m subplots (hence, 80 subplots per field) within which weed absence/presence per species was recorded [41]. We estimated weed species abundance by the sum of the occurrence of each plant species per field (from 0 to 80). Weed abundance per field was assessed by summing weed species abundance for all species present in the field.

(d) Landscape metrics and meteorological data

As landscape may modify the relationships between insecticide intensity and ecological function [27,32–34], we evaluated the effect of landscape context on the relationship between insecticide intensity and natural pest control or pest/weed abundance. We extracted landscape composition metrics around sampled field by focusing on three landscapes features: meadows, which included grassland either herbaceous or mixed (with legumes), crop diversity and oilseed rape. These landscape features have already been identified as key parameters affecting oilseed rape natural pest control services and pest abundance in agricultural landscapes [28,42,43]. They were calculated at five different radii ranging from 500 to 2000 m from the centroid of focus fields [43,44]. Crop diversity was calculated by Shannon index using seven crop categories: cereal, oilseed rape, maize, sunflower, pea,

ryegrass and all other arable crops (<1.5% of total area in the 2000 m buffer). Pairwise Pearson correlation coefficients between all landscape metrics never exceeded $|r| = 0.29$ whatever the scale of landscape measures.

We also accounted for the meteorological context as it can explain oilseed rape yield variation between years as well as for insect pest/weed abundance or natural pest control [45–48]. For that, we extracted temperature and precipitation from the European Climate Assessment & Dataset (https://www.ecad.eu/) that provides mean monthly temperature and sum of precipitation (also per month) into 10 × 10 km^2 grid cells. This monthly scale was used in previous studies on the effect of weather on oilseed rape yield [45,46].

(e) Farming practices

Data on crop yields and farming practices were collected each year during interviews conducted with farmers after harvest. We estimated fertilizer intensity for each field considering nitrogen, phosphorus and potassium inputs. The amount of inorganic fertilizer used was directly calculated from the fertilizer composition and the quantity applied, while the quantity of fertilizer mineralized from organic fertilizers was deduced using the method described in [49]. Fertilizer-use intensity was the sum of nitrogen, phosphorus and potassium, all standardized by their mean value before their sum.

Pesticide use was first assessed using the mass of active ingredients per hectare (QA, g ha^{-1}), but we also computed the treatment frequency index (TFI) [50]. This standardized quantitative index allows comparisons of pesticide-use intensity between fields, as TFI measures the intensity of applications as the dosage applied per unit of cultivated area divided by the recommended dosage per crop type as provided under national guidelines [50]. To calculate TFI values, we used the annual recommended dose from the official French database on registered pesticides (https://ephy.anses.fr/). See [51] for a detailed description of the computation of the TFI indicator. For the two indicators, we computed TFI and the mass of active ingredients for all pesticides and per type (i.e. herbicide and insecticide). While fungicides are applied in oilseed rape fields, we did not account for them in our study as we only focus on insect pest and weed regulation.

(f) Statistical analyses

(i) Total effect of insecticide use on oilseed rape yield

We first investigated the total effect of insecticide on oilseed rape yield. We used linear models (LMs) with yield (expressed as ton ha^{-1}) as the dependent variable, and data collected through farm surveys on the 383 fields. Insecticide use was added as explanatory variable as well as its quadratic term to test for a nonlinear relationship with yield. Two different LMs were used, with either QA or the TFI as explanatory variables assessing insecticide use, and were compared based on AIC (Akaike information criterion). The pesticide index from the model with the lowest AIC was used for the rest of analyses. In these models, we also added fertilizer use intensity, herbicide use and their quadratic terms as covariates in addition to soil type, and mean monthly temperature and sum of monthly precipitations into models to take into account yield variability due to different climatic conditions between years. We selected the most appropriate time windows for computing the mean monthly temperature and sum of monthly precipitation using the 'climwin' package [52]. 'Climwin' algorithm tests all possible combination of time windows between sowing (estimate starting from 1 August in our study site) and harvesting (31 June) period on oilseed rape yield in LMs accounting also for other variables and compared them based on their AIC values [53] to select the best period. For all models, we performed a backward–forward stepwise selection on AIC to keep only informative variables.

(ii) Direct effect of insecticide use on natural pest control and insect pest or weed abundance

Next, we built four LMs to analyse the direct effects of insecticide use on insect and weed abundance, and on predation rates of insect pests and weeds. Meadows, oilseed rape and crop diversity were added to each model (as landscape covariates), and insecticide use was included as a linear and quadratic term. To account for nonlinearity of effects, we could have used generalized additive models (GAMs) as an alternative option. Using GAM (with a maximum knot of three to avoid over-fitting) rather than polynomials did not change the pattern of relationships (see electronic supplementary material, figure S2) and thus we present the results by modelling relationships with quadratic terms. In addition, several covariates were added in each model. For the weed abundance model, we added herbicide use and its quadratic term. We also included interaction between insecticide use (or herbicide use in the case of weed) and landscape variables as effect of landscape may modulate the effect of insecticides [28,32]. Relevant spatial scales (from 500 to 2000 m) for landscape variables were selected based on the AIC for each model and the model with the lowest AIC score was retained as the best model. Buffers selected for each variable are presented in electronic supplementary material, table S2. Spatial extents of the selected buffers were respectively 500 and 750 m for insect predation rate and insect pest abundance and 2000 and 1000 m for seed predation rate and weed abundance. Field size, the mean monthly temperature and sum of monthly precipitation, which were found to modify natural pest control in previous studies [28,47,48], were thus also added as covariates. For all models, we performed a backward–forward stepwise selection on AIC to keep only informative variables.

(iii) Indirect effect of insecticide use on yield through natural pest control and pest abundance

To identify the potential cascading effect of insecticide use on yield due to indirect effect on pest abundance or through natural pest control (figure 1), we used a SEM [54]. We used data from the 115 fields with both insect pest and weed abundance and measures of their predation rate. We decomposed the total effect of insecticide on oilseed rape yield throughout four indirect effects of insecticide on insect pest/weed abundance and insect/seed predation rate (figure 1). We used LMs to fit the SEMs. Insect pest/seed predation rates were both explained by insecticide intensity, temperature, precipitation and field size. Insect pest/weed abundance were both explained by insecticide intensity and, respectively, by insect pest and weed seed predation rates (figure 1) as well as temperature, precipitation and field size. Herbicide dose was also added as covariate for weed abundance. Yield was explained by soil type, fertilizer and its quadratic term, as well as insect pest and weed abundance. A second SEM was run by adding landscape metrics and their interaction with insecticide to understand how insecticide modulates the effects of landscape on insect pest/seed predation or predation rates. For the SEMs, the causal structure of models was obtained by using a backward–forward stepwise selection on AIC, to remove non-informative pathways. In addition, we ensured that no path was missing with Fisher C′ test. The results showed that none were missing (all $p > 0.18$).

All analyses were performed with R 4.3.0 [55]. Weed abundance and seed predation were squared-transformed and insect pest abundance was log(x+1) transformed to improve normality and homoscedasticity of model residuals as proposed by Martin *et al.* and Brown *et al*. [56,57]. For insect predation rate, we used log((1 − predation rate)+1) because of right-skewed distribution of data. In the figure and table from this model, we inversed coefficients in reported results for the sake of understanding. To ensure the validity of our modelling choice, we made visual inspections of the residual distribution (normality and homogeneity of variance) and statistical tests associated to the 'DHARMa' package test for over/under dispersion of residuals [58]. No over/under dispersion of residuals was found (all $p > 0.63$; see electronic supplementary material, figure S3). We also square-rooted insecticide and herbicide inputs the distributions of which were right-skewed. As insecticide is the variable of interest in this study, we always keep it in the final model. We checked for spatial autocorrelation in the residuals of models using Moran's index for predation rate and pest abundance models. Spatial autocorrelation was only detected for the yield model (Moran I = 1.70, $p = 0.04$). For this model, we realized an alternative one with accounting for spatial autocorrelation with a spatial Gaussian structure. As results did not differ when accounting for spatial autocorrelation, we decided to report outputs of the model without a spatial Gaussian structure (electronic supplementary material, table S3). Variance inflation factor (VIF) was used to check for collinearity between explanatory variables, and none was found (all VIF < 1.8). When a quadratic relationship was detected between insecticide use and insect pest/weed abundance or predation rates, we used an additional regression model with break-points with the same model structure as that for LMs thanks to the 'segmented' package to identify the break-point at which the relation reversed itself [59]. The R package 'spdep' was used for the calculation of Moran's index, 'stat' for LMs, 'piecewise SEM' for SEM models, 'MASS' for stepwise selection and 'car' package for VIF. Residuals of models were visually checked and no heteroscedasticity was observed.

3. Results

On average, 136.0 g ha^{-1} (min–max = 0–1190.0 g ha^{-1}) of insecticide active ingredients was applied in the surveyed oilseed rape fields, corresponding to an average TFI of 2.46 (0–7.23). The dose and the TFI were positively correlated (Spearman correlation: $\rho = 0.60$, d.f. = 381, $p < 0.001$). On average, 1623.0 g ha^{-1} (0–4123.0 g ha^{-1}) of herbicide active ingredients were applied, corresponding to an average TFI of 1.90 (0–5.74) with a strong positive correlation between them ($\rho = 0.68$, d.f. = 381, $p < 0.001$). Insecticide and herbicide use were also positively correlated (for dose: $\rho = 0.30$, d.f. = 381, $p < 0.001$; for TFI: $\rho = 0.25$, d.f. = 381, $p < 0.001$). Nitrogen use varied from 20 to 270.4 kg ha^{-1} (average = 155.3 kg ha^{-1}), phosphorus from 0 to 182 kg ha^{-1} (57.9 kg ha^{-1}) and potassium from 0 to 365 kg ha^{-1} (38.3 kg ha^{-1}). Fertilizer intensity was not related to soil type (ANOVA, all $p \geq 0.11$).

The average predation rate per card was 59.2% (s.d. = 28.9) for insect pests and 30% (21.85) for weed seeds. Insect and seed predation rates were positively correlated among fields ($\rho = 0.23$, d.f. = 113, $p = 0.013$). Insect pest abundance ranged between 0 and 30.5 individuals per field (average = 3.48 insects per field) mainly composed of flea beetles (52.8%) and weevils (28.6%), followed by aphids (12.7%), pollen beetles (4.8%) and leafhoppers (1.1%). Weed abundance ranged from 15 to 412 individuals per field (average of 161.2 individuals per field) belonging to 182 species with mainly *Fallopia convolvulus* (9.8%), *Mercurialis annua* (8.5%), *Viola arvensis* (7.1%), *Polygonum aviculare* (4.9%) and *Alopecurus myosuroides* (4.5%). Insect pest and weed abundances were also positively correlated ($\rho = 0.28$, d.f. = 113, $p = 0.003$).

(a) Total effect of insecticide use on oilseed rape yields

The model using active ingredients to characterize insecticide use better explained yield (AIC = 742.3) than the model using TFI (AIC = 787.4). As predicted, we found that the total effect of insecticide use on yield had a nonlinear concave relationship between insecticide use and oilseed rape yield (figure 2A; see electronic supplementary material, table S4, for associated statistics). We found a saturating effect of insecticide use at a threshold of about 36.2 g ha^{-1} (95% CI = 22.0–53.9; figure 2A). This nonlinear effect was only observed when insecticide use was estimated with the dose (figure 2A), as no significant relationship between crop yield and TFI was observed (electronic supplementary material, figure S4, table S4). In addition, oilseed rape yield increased with fertilization intensity, also showing a concave effect (figure 2C; electronic supplementary material, table S4). Oilseed rape yield also increased with herbicide dose (figure 2B; electronic supplementary material, table S4). Mean monthly

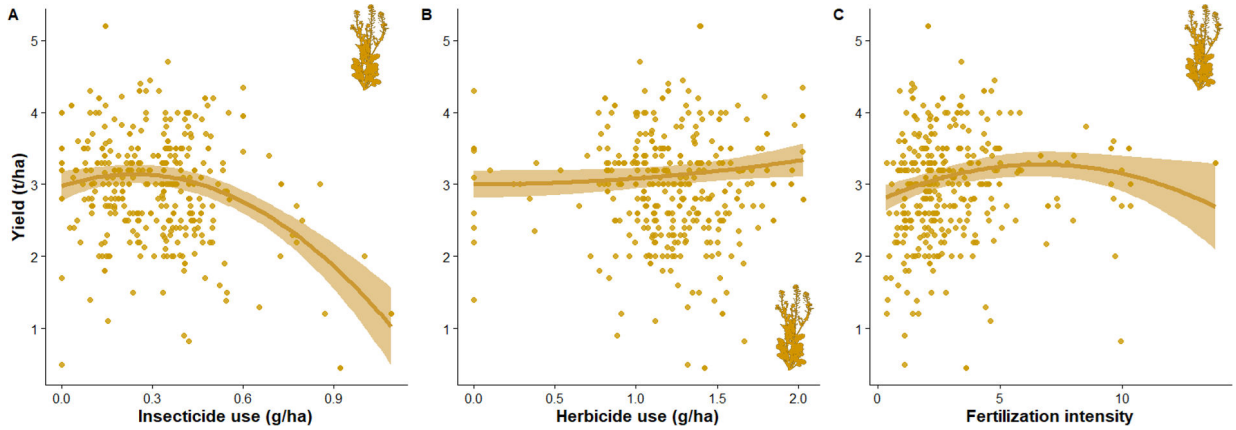

Figure 2. Observed relationships between (A) insecticide use, (B) herbicide use and (C) fertilization intensity with measured yield ($n = 383$). Insecticide use was estimated by insecticide active ingredient squared-root transformed. Fertilization intensity is the sum of nitrogen, phosphorus and potassium scaled by their mean (see §2). Dots represent raw data and lines represent relation predicted by LMs (see §2). Shaded areas show confidence intervals at 95%.

temperature and sum of monthly precipitations were also found to increase oilseed rape yield (electronic supplementary material, table S4), and higher yields were found in red soils (3.9 t ha^{-1}) than in calcareous soils (3.2 t ha^{-1}).

(b) Direct effect of insecticide use on natural pest control and insect pests or weed abundance

We found a positive, nonlinear relationship between insecticide use and insect abundance, with pest abundance starting to increase from 14.5 g ha^{-1} (95% CI = 6.3–26.1 g ha^{-1}; figure 3A; see electronic supplementary material, table S5, for associated statistics), i.e. a lower threshold than the breakpoint from which yield started to decrease. Insect pest control similarly decreased nonlinearly from about the same threshold value, 14.4 g ha^{-1} (95% CI = 4.4–30.1 g ha^{-1}; figure 3B; electronic supplementary material, table S5). A linear negative relationship was found between insecticide intensity and weed seed predation (figure 3D; electronic supplementary material, table S5), although the relationship was unexpectedly quadratic between insecticide intensity and weed abundance, with a threshold value at about 3.2 g ha^{-1} (95% CI = 0.9–6.6 g ha^{-1}; figure 3C; electronic supplementary material, table S5).

(c) Interactive effects of insecticide use and landscape context on natural pest control and pest abundance

Interestingly, our models revealed that the effect of insecticides on seed predation and insect abundance was modulated by crop diversity at landscape scale, but with opposite effects (electronic supplementary material, figure S5). A negative effect of insecticide use on seed predation was only observed at a low level of crop diversity and became neutral or positive at a higher level (electronic supplementary material, figure S5A, table S5). Conversely, a positive effect of insecticide use on seed predation was more important at lower than at higher crop diversity (electronic supplementary material, figure S5B, table S5). This interactive effect of insecticides with landscape features was not observed for other landscape metrics. Only simple linear effects of landscape were observed (electronic supplementary material, table S5). More specifically, insect predation rates increased with the proportion of oilseed rape, while seed predation rate decreased with meadow abundance (electronic supplementary material, figure S6, table S5).

(d) Indirect effect of insecticide use on yield through natural pest control and pest abundance

In order to disentangle the different indirect effects of insecticide use on yield, we used SEM. SEM showed that the direct positive effect of insecticide use on insect pest abundance (figure 3A) was mediated by an indirect negative effect of insecticides on natural pest predation rate (figure 4). Natural pest control reduced insect pest abundance by 72.0% in fields with highest seed and insect pest predation rates compared with those with the lowest ones (electronic supplementary material, figure S7). In addition, pest predation rate was 29% lower in fields with high insecticide use compared with those with a low use and no direct effect of insecticide use on insect pest was detected. Consequently, insect pest abundance was higher in the fields with high insecticide use (figure 4). The positive direct effect of insecticide use on weed abundance (figure 3C) was mediated both by a slight indirect negative effect of insecticides on natural pest predation rate as well as a direct effect of insecticide on weed abundance (figure 4). Natural pest control reduced weed abundance by 34.8% (electronic supplementary material, figure S7), comparing fields with the lowest and highest seed predation rate. Insect seed predation rate was reduced by 12% by insecticide between fields with low and high insecticide use resulting in a positive relationship between insecticide use and weed abundance in the SEM (figure 4). In addition, we found that weed and insect pest abundance reduced yield up to 21.4 and 25.1%, respectively (figure 4; see electronic supplementary material, figure S8, for relation between insect pest or weed abundance and yield). Adding landscape variables to SEM showed that insecticides actually decreased the positive effect of landscape on natural pest control, by reducing the positive effect of meadow and crop diversity, respectively, on insect and seed predation (electronic supplementary material, figure S9). We also observed direct effects of insecticide on insect abundance in

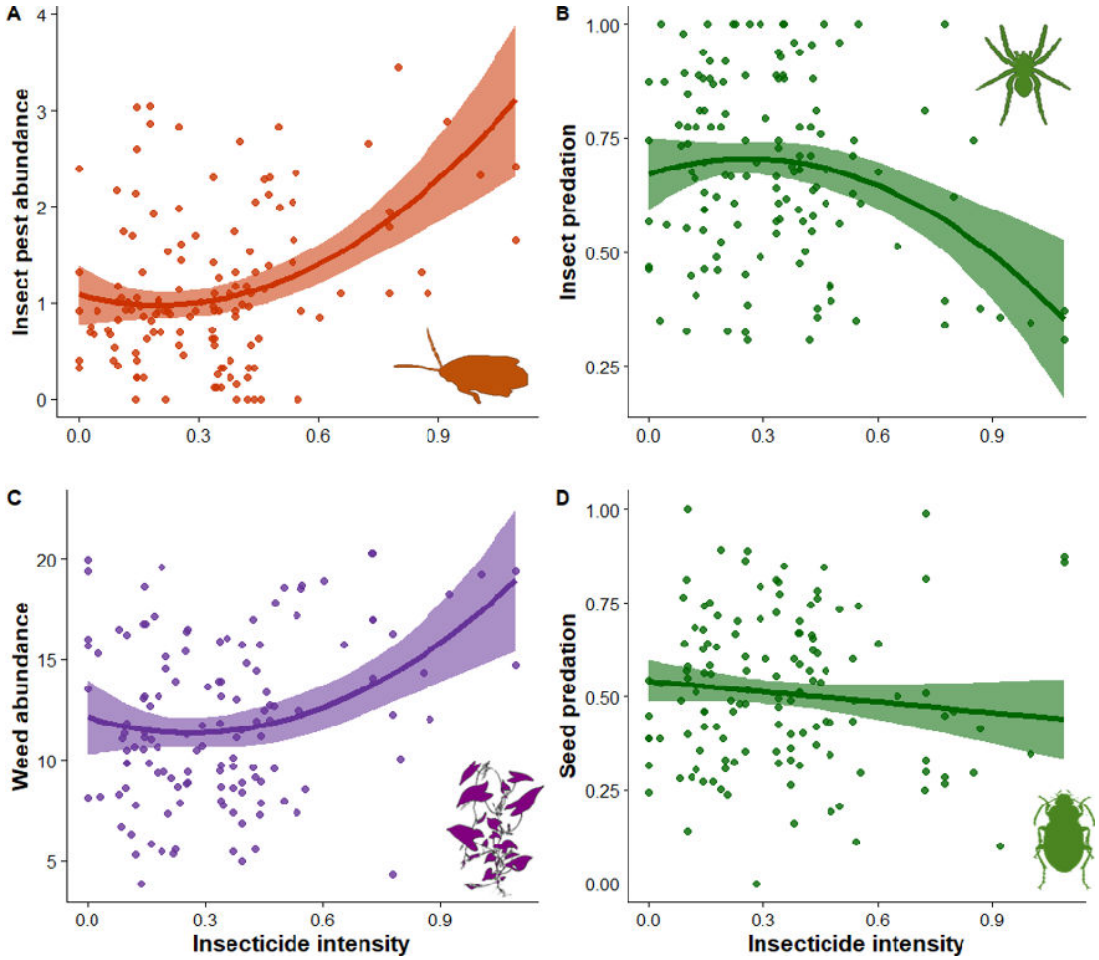

Figure 3. Relationships between insecticide use and (A) insect pest abundance or (B) weed abundance, as well as with (C) insect predation rate and (D) seed predation rate. Insecticide use was estimated by the amount of insecticide active ingredients applied (in g ha^{-1}) squared-root transformed. Dots represent raw data and lines represent the relationship predicted by LMs (see §2). Shaded areas show confidence intervals at 95%.

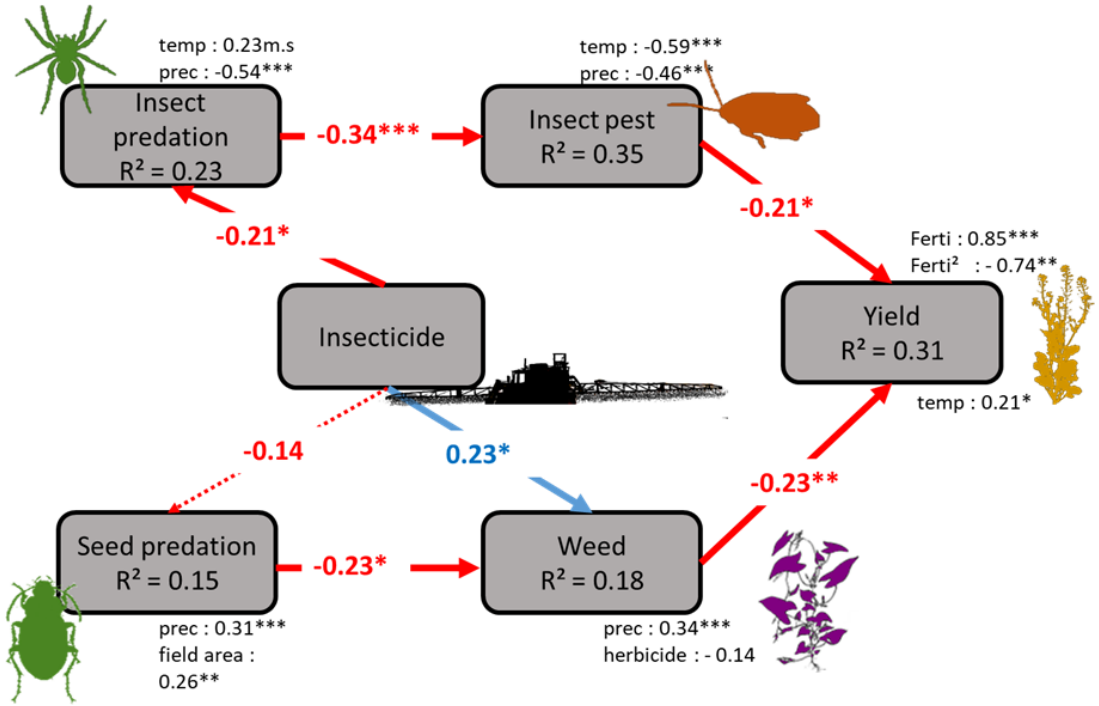

Figure 4. Results of SEM depicting the direct and indirect effects of insecticide on insect and weed abundances through their effects on insect and weed predation rate as well as this cascading effect on yield. Pesticide use was estimated by the amount of active ingredients applied (g ha^{-1}). Solid arrows represent significant relationship and dotted non-significant relationship. Negative relationships are in red and the positive ones in blue. Standardized estimates are given as well as their level of significance: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$. The variable 'prec' refers to precipitation and 'temp' refers to temperature.

interaction with the landscape context (electronic supplementary material, figure S9). Insecticide increased the positive effect of crop diversity on abundance of insect pests while reducing the negative effect of oilseed rape proportion on the same metrics. Globally, SEM showed that the total effect of insecticide use observed on oilseed rape yield (figure 2A) was mediated by the indirect effect of reduction of natural pest control (figure 4).

4. Discussion

Our study reports a nonlinear relationship between the intensity of insecticide use and yield of oilseed rape leading to an overall negative net effect of high insecticide use on crop productivity. We provide compelling evidence that this negative effect is mainly mediated by deleterious impacts of insecticide on natural enemy communities and the pest control services they deliver. Our analyses indicate that above a certain threshold of insecticide use intensity (estimated here at 36 g ha^{-1}), the negative impact of insecticides on natural pest control exceeds the beneficial effect of chemical pest control on crop productivity observed at low levels of insecticide use. In addition, our study reveals that specific landscape-scale management options based on increased proportion of meadows and crop diversity can buffer the negative effects of insecticides on natural pest control and support crop productivity.

We found that pesticide use can indirectly constrain oilseed rape yields because of negative impacts on natural pest control. Previous theoretical and empirical studies have already demonstrated that an increase in insecticide use can reduce natural pest control and increased pest abundance [11,12,23,60]; however, our study further demonstrates that these negative effects cascade down to limit crop productivity. In addition, we identified a threshold above which insecticide use limits natural pest control and leads to lower yields. This threshold was estimated at 36 g ha^{-1} of active ingredients. Previous field studies showed that pyrethroids, the main insecticide class used in 96% of the fields (368 of 383 fields) of the study (see electronic supplementary material, table S6, for a complete list of insecticide active ingredient use), has a lethal dose (that causes the death of 50% of the studied group) of <20 g ha^{-1} for most natural enemies (see review in [61]). In our study site, the amount of pyrethroids applied varied between 0 and 153.5 g ha^{-1} (mean: 38.4 g ha^{-1}, median: 28 g ha^{-1}). Moreover, most of the fields were sprayed by more than one class of pesticide (218 of 383 fields, i.e. 56.9%). While our study reports a major negative effect of insecticides on natural enemies in real-field conditions, it also demonstrates that the same applies for natural weed control, a neglected aspect of pest control services. The impact of insecticide intensity on natural weed control has rarely been investigated, but natural predators of weeds, such as carabids, overwinter in oilseed rape fields [30,62] and are consequently significantly exposed to insecticide use. Our path modelling showed a positive effect of insecticide intensity on weed abundance that was not completely explained by the reduction of weed natural pest control. Possibly, our sentinel prey cards did not reflect all weed natural pest control as weed seeds can also be controlled by other organisms such as soil microorganisms [63] or small mammals [64] that are also negatively affected by insecticide use [65,66].

Intensive agricultural landscapes supporting high use of insecticides are known to reduce biodiversity and ecosystem services [4]. Interestingly, our study further indicates that key management options based on landscape diversification through amount of meadows and crop diversity can buffer the negative effects of pesticides on natural pest control services, confirming previous studies [27,32–34]. Indeed, landscapes with significant amount of meadows and a greater diversity of crops increase the spatiotemporal continuity in key resources for natural enemies such as food, alternative hosts or shelters [67,68], which can explain this buffering effect.

Some limitations of our study warrant further analyses. First, the cascading negative effects of insecticide use on crop yields might have been reinforced by insecticide resistance of oilseed rape pests to insecticide [69]. We did not record the level of pest resistance in our case study and this may have contributed to the observed pattern. However, our analyses clearly highlight that intensive insecticide reduces the abundance of natural enemies which undoubtedly limit top-down control of pests and therefore increase yield losses. Second, the different indices of pesticide we used did not account for actual toxicity of active ingredients but only considered the intensity of pesticide use. Identifying the most toxic pesticides driving the detected negative relationship between insecticide use and natural pest control appears now as a major research avenue.

The reduction of risks associated with pesticide use and the transformation of agri-food systems towards low pesticide production systems are important goals for society, policymakers and food-value chain actors [51,70]. In this study, taking advantage of a large monitoring programme in 383 farmers' fields over 10 years, we showed that increasing insecticide intensity in oilseed rape production beyond certain thresholds (36 g ha^{-1}) actually decreases total pest control and yields, through its negative effects on natural pest control. This implies that insecticide intensity beyond these thresholds not only has adverse environmental effects and additional (application) costs for farmers, but also has negative effects on overall crop production levels. More studies like the one conducted here are needed to understand the genericity of the observed pattern but in other contexts, and demonstrate that reducing pesticide use can yield win–win strategies, benefiting both agricultural productivity and environmental sustainability. Investigating the economic cost of insecticide overuse by combining the expenses of insecticide application with the yield losses incurred by farmers could serve as an incentive to promote reduced usage.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data are available [71].

Electronic supplementary material is available online [72].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. T.P.: conceptualization, data curation, formal analysis, investigation, validation, visualization, writing—original draft, writing—review and editing; N.M.: conceptualization, data curation, validation, writing—original draft, writing—review and editing; A.R.: conceptualization, funding acquisition, investigation, supervision, validation, writing—original draft, writing—review and editing; S.G.:

conceptualization, funding acquisition, investigation, methodology, supervision, validation, writing—original draft, writing—review and editing; V.B.: conceptualization, funding acquisition, investigation, methodology, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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