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RESEARCH ARTICLE

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Spatiotemporal isolation of oilseed rape fields reduces insect pest pressure and crop damage

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Abstract

- 1. Pest management is essential to maintain agricultural production, but recent shifts in policies and the development of insecticide resistance have restricted the availability of insecticides for pest suppression. Identifying the landscapelevel resource requirements of pests to complete their life cycles might unveil new sustainable solutions to regulate their populations and prevent crop damage.
- 2. We assessed the effects of landscape composition and configuration at different spatial scales on flea beetle densities and crop damage in 56 spring oilseed rape fields sampled over 5 years in Sweden. We considered the cover of non-crop habitats as an aspect of landscape composition and the distances to the host crop and an alternative host crop in the previous year, edge density and crop diversity as aspects of landscape configuration.
- 3. The distance from spring oilseed rape in the previous year reduced flea beetle densities and crop damage across most species and spatial scales. Edge density reduced the densities of two flea beetle species, predominantly at the 500m radius landscape scale. The cover of forests and permanent pastures as well as crop diversity in the previous year increased the densities of different species at several, mostly larger (1000-2000m) spatial scales. Increasing permanent pasture cover at the 500 m scale also increased crop damage.
- 4. Synthesis and applications: We find that there is no one fits all approach in designing landscapes for flea beetle regulation as habitat use and scales of effect are species-specific for these pests. However, increasing the spatiotemporal isolation of host crop fields is a promising and potentially more general means of disrupting pest populations and reducing crop damage. Considering the ecological traits of the pest species is a possible next step to optimise landscape-based pest management.

KEYWORDS

Brassica napus, flea beetles, insect pest management, landscape structure, legacy effect, neonicotinoid ban, Phyllotreta, semi-natural habitat

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1 | INTRODUCTION

A substantial share of agricultural production is lost to crop pests every year (Savary et al., 2019). Current practices in temperate agricultural landscapes rely heavily on the application of chemical pesticides to suppress pest outbreaks (Popp et al., 2013). However, pesticides can have negative effects on non-target organisms (Rundlöf et al., 2015) and evidence for large-scale biodiversity declines in temperate agricultural regions is growing (Seibold et al., 2019). As a result, policymakers have begun to re-evaluate approved pesticides, which, for instance, has led to the ban of neonicotinoid insecticides in the European Union (Kathage et al., 2018). With a narrowing pesticide spectrum, pesticide resistance is becoming increasingly problematic. For instance, many insect pests had already developed resistance against older alternatives to the recently banned neonicotinoid insecticides and new cases of insecticide resistance are continuously emerging (Zheng et al., 2020). With the perspective of insecticides no longer being a reliable solution for the suppression of insect pests and a growing awareness of the negative impacts on the environment, crop production is in dire need of sustainable pest management alternatives (Deguine et al., 2021).

The sustainable regulation of insect pest populations could be promoted by managing the composition and configuration of agricultural landscapes. Pests could be controlled bottom-up by disrupting their access to resources needed to complete their life cycle, such as availability of host plants, alternative hosts or overwintering sites (Han et al., 2022). Simultaneously top-down regulation by natural enemies depends on habitat and resource availability, which, in turn, is affected by aspects of landscape composition, such as the amount of perennial habitat, and configuration such as mean field size (Martin et al., 2019). Current agricultural landscapes are a product of land use transformation streamlined towards labour and cost-efficient agricultural production rather than pest regulation (Foley et al., 2005). With the dearth of chemical pest control options, the composition and configuration of agricultural landscapes could gain importance for pest regulation.

For landscape composition, especially non-crop and semi-natural habitats are often important in insect pest life-cycles with the effects of specific habitats depending on the ecology of the pest species and their habitat requirements (Karp et al., 2018; Tamburini et al., 2020). Extensively managed perennial non-crop habitats such as forest edges, grasslands, permanent pastures and field edges can serve as overwintering habitats for pests (Ekbom, 2010; Tscharntke et al., 2016). The effects of non-crop habitats on pests and crop damage are, however, ambiguous. Higher non-crop habitat cover is occasionally found to reduce pest pressure, likely due to pest dilution in diverse landscapes and simultaneously increased top-down control by natural enemies (Rusch et al., 2016; Tamburini et al., 2020). Despite information amassing on the relation between pests and non-crop habitat cover, there is a lack of information on species-specific interactions with different non-crop habitats and resulting effects on crop damage.

Apart from non-crop habitats, also agricultural fields and the land covered by host crops in the previous season can increase pest densities (Delaune et al., 2021). Pest populations build up in the host crop during the growing season and several economically important pests overwinter in suitable structures near host crop fields or directly in the field (Burgess, 1981; Sutter et al., 2018). In the following season, crop pests emerge from these overwintering sites and disperse to the closest suitable host crop with an expectable distance decay (e.g. Hederström et al., 2022). The land covered by host crops or the distance to host crop fields in the previous season might thereby determine pest densities colonising host crop fields in the following season, but this is not well explored for many pest species.

The effects of landscape configuration on pest populations are less well understood. Landscape features such as the diversity of cultivated crops and the density of perennial edges, a measure of overall patch and field sizes, were shown to be positively related with natural pest control, the latter also negatively with pest densities (Martin et al., 2019; Redlich et al., 2018). Both aspects might thereby render top-down regulation of pest populations. Habitat edges, however, could also serve as overwintering sites for pests. The net outcome of bottom-up and top-down effects on crop pest populations from landscape-level crop diversity and edge-density need to be clarified.

With different aspects of agricultural landscapes related to both bottom-up and top-down pest control, strategic land-use planning at the landscape level could be a step towards sustainable pest management (Lundin et al., 2021). Our aim here was to identify landscape-level drivers of pest densities and crop damage as well as their spatial scales of effect, that is the scale at which management would be needed. While previous studies investigated the effects of landscape composition and configuration in the same year on insect pests in winter oilseed rape (e.g. Zaller et al., 2008), an assessment of legacy effects of landscape structure is lacking for spring oilseed rape. We analysed 5 years of data on flea beetle (Coleoptera, Alticinae) densities and associated crop damage in spring oilseed rape collected in south-central Sweden. We expected that pest densities and crop damage (i) increase with the availability of source habitats for pests, that is non-crop overwintering habitat such as forests and pastures, and alternative host crops that could have provided food and undisturbed refuge for overwintering such as winter oilseed rape fields, (ii) decrease with increasing distance to the host crop in the previous year, as increasing isolation hinders colonisation of spring oilseed rape fields in the following year, and (iii) decrease with increasing crop diversity and edge density, as both have been shown to benefit natural pest control (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Study system

Oilseed rape *Brassica napus* is an important cash crop worldwide, but yields are limited by several pests (Williams, 2010). Flea beetles (Coleoptera, Alticini) attack oilseed rape plants at the cotyledon stage (Williams, 2010). Spring oilseed rape, an important cash crop in boreal agriculture, is vulnerable to attacks by a complex of several flea beetle species of the genus *Phyllotreta* at emergence (Ekbom, 2010). These beetles overwinter as adults, emerge in



FIGURE 1 Assumed relationships between different aspects of landscape composition and configuration and pest densities as well as crop damage under the assumption that pest densities are positively related to crop damage (+/green: positive; -/red: negative). Landscape aspects that favour pest overwintering such as the cover of non-crop habitats (e.g. forests or pastures) or the availability of alternative host crops should be positively related to pest populations. Increasing distance to the host crop in the previous season should hinder colonisation in the following season and thus be negatively related to pest populations. Landscape aspects that favour natural pest control like edge density or crop diversity should be negatively related to pest populations mediated by their assumed positive effects on natural enemies. All positive effects on pests should result in increased crop damage and negative effects on pests should result in reduced crop damage.

early spring depending on soil temperature, subsequently move to spring oilseed rape fields where they feed on the newly emerged cotyledons and stems and lay their eggs on the soil near the stems (Ekbom, 2010). The larvae subsequently feed on the roots of the young plant (Ekbom, 2010). The feeding damage to seedlings caused by flea beetle attacks early in the season is directly linked to yield losses (Lundin, 2020). Natural enemies of flea beetles include both specialised parasitoid braconid wasps as well as generalist predators such as carabid beetles, lacewings and spiders (Ekbom, 2010). To control these early season pests, neonicotinoid seed treatments have long been used. However, in 2013, the European Union banned neonicotinoid seed treatments (Kathage et al., 2018), which has created the need to identify new strategies for effective pest control.

2.2 | Study design

We assessed flea beetle densities and cotyledon damage in 56 spring oilseed rape fields over 5 years from 2014 to 2018 (2014: 5

fields; 2015: 8 fields; 2016: 9 fields; 2017: 19 fields; 2018: 15 fields). All study sites were located in Stockholm, Uppsala and Västmanland counties in south-central Sweden (Figure 2). This region is characterised by agricultural production and a high proportion of embedded forest fragments. Field sizes of the selected fields ranged from 2.10 to 55.24 ha (mean \pm SE: 17.56 \pm 2.35 ha). No-till fields were not included as flea beetle densities and oilseed rape damage are reduced in such fields (Lundin, 2019). Permission for this study was obtained from landowners. Fields were sown with spring oilseed rape without insecticide seed treatments between 11 April and 26 May depending on the field and year.

In each field, we established a sampling plot. The distance of the sampling plot to the nearest field edge varied between fields due to local conditions (mean: 31.0 ± 2.9 m; 9 to 102 m; centre of sampling plot to field edge) but was not significantly correlated with any of the responses (Pearson's |r| < 0.21; p > 0.05) and should therefore not bias our analyses. The sampling plots varied slightly in size among sites and years due to local limitations (length: 52.1 ± 1.2 m; 28-112 m; width: 23.9 ± 0.4 m; 12-30m; area: 1229.9 ± 19.7 m²;



FIGURE 2 Map showing the location of the study region in south-central Sweden (left) and the distribution of the fields within the study region with the years represented by different colours (yellow: 2014; orange: 2015; red: 2016; blue: 2017; 2018: purple).

672–1440 m²). No foliar insecticides against flea beetles were used in the sampling plot during the experiment, but apart from that, the sampling plots were managed by the farmer identically as the rest of the field, including herbicide applications.

2.3 | Land-use mapping

Land-use data were obtained from digitalised map layers 'Terrängkartan' (Lantmäteriet, 2018) and crop information from a layer provided by the Integrated Administration and Control System, administered by the Swedish Board of Agriculture. In this layer, information about the cover of crops grown is given for all fields. For our analyses, we followed the crop categorisation into 14 crop classes used by Raderschall et al. (2021) (Table S1 in Supporting Information).

We extracted land-use types on three buffer radii, 500, 1000 and 2000m, around the sampling plots to investigate their scales of effect. The 500 and 1000m radii emerged as scales of effect in previous studies on flea beetles (Perez-Alvarez et al., 2018; Snyder et al., 2021) and we included the 2000m radius to check whether effects occur on scales beyond the ones previously assessed. The minimum distance between sampling plots in any year was 2460m, resulting in no overlap in landscapes with 500m or 1000m buffers, but slight overlap in five landscapes ranging from 6.1 to 27.4% in the 2000m buffer. Within each buffer, we measured potential overwintering sites in the form of (i) non-crop habitats (forest and permanent pasture cover) and (ii) the absolute distance to the nearest alternative host crop field (winter oilseed rape that could have been colonised at cotyledon stage in the previous autumn). (iii) We calculated the absolute distance to the closest spring oilseed rape field in the previous season (Table S2) as a potential source of flea beetles in the following season. We used distance instead of cover for oilseed rape fields as they were absent in more than 43% of the landscapes at all scales (Table S1) making isolation more informative than cover compared to forests and pastures that were widely distributed in various smaller fragments in all landscapes. Distances were measured between the centres of the sampling plot and the farm block containing oilseed rape. Additionally, we measured two landscape metrics positively associated with natural pest control: (iv) edge density measured as the total edge-length of patches under agricultural land-use within the respective buffers and (v) the Shannon index of crop diversity in the previous year calculated across the 14 crop classes (henceforth: crop diversity), as overwintering flea beetle densities are affected by pest control in the previous year.

2.4 | Data collection

Flea beetle densities were assessed using pitfall traps (Perez-Alvarez et al., 2018). In each sampling plot, we placed four pitfall traps (height: 11 cm, diameter: 11.5 cm) filled with ~500 mL water with a few drops of odourless detergent to reduce surface tension, one in each corner of the sampling plot distanced 1 m from the plot edges, resulting in a minimum distance of 10 m between pitfall traps. Pitfall traps were installed and activated within 1 week after crop sowing before any plants had emerged. They were emptied every 2-4 days until the crop had two fully developed true leaves, resulting in 9-46 days of pitfall trapping per trap as oilseed rape growth rate varied across sites and years. The total pitfall trap days per sampling plot

ranged from 48 to 181 days with all four traps combined (mean \pm SE: 112.1 \pm 4.1 days). The sampling did not require ethical approval.

Pitfall trap samples were sorted in the laboratory and flea beetles were identified to species or genus level (Table S3). As flea beetle numbers were exceptionally high in 2014 and 2015, not all individuals could be identified. In these years, we counted all flea beetles in each sample, identified the first 20 individuals in each sample and extrapolated the species distribution in the samples containing more than 20 individuals. For subsequent analyses, the samples from all four traps per sampling plot and throughout the sampling period were pooled, resulting in one measure per sampling plot and field. In our analyses, we included only species and genera that comprised at least 10,000 individuals across all years, which were the genus *Phyllotreta* and four species therein (*P. atra, P. striolata, P. undulata, P. vittula*) that are known oilseed rape pests (Ekbom, 2010) and the genus *Chaetocnema* which was abundant and also observed on cotyledons in the field (Table S3).

Cotyledon damage caused by flea beetles has a characteristic shot-hole appearance (Brandt & Lamb, 1993) and accumulates during crop growth. We classified cotyledon damage visually following the crop damage classes in Lundin (2020) at the time point of the last pitfall trap collection, that is at the end of the cotyledon stage. Cotyledon damage was assessed in 16 (in 2014, 2015 and 2016) or 10 (in 2017 and 2018) randomly placed 0.25 m² quadrats within each sampling plot on five randomly selected plants per quadrat, thus on a potential total of 80 or 50 plants per sampling plot. The actual number of plants assessed was somewhat lower because quadrats in some cases contained less than five plants (mean \pm SE: 78.7 \pm 0.9 in 2014 to 2016, 39.6 \pm 2.4 in 2017 and 2018). For the analyses, we back-transformed crop damage class values into proportion of cotyledon damage using the centre points of each damage class and calculated the mean damage over all plants assessed per sampling plot.

2.5 | Statistical analyses

All statistical analyses were performed in R 4.1.2 for Windows (R Development Core Team, 2021). For all analyses, data were pooled at the sampling plot level. We tested the responses 'all flea beetles', 'Phyllotreta sp.', 'P. atra', 'P. striolata', 'P. undulata', 'P. vittula', 'Chaetocnema sp.' and 'crop damage' against the continuous fixed effects 'forest cover', 'pasture cover', 'minimum distance to winter oilseed rape in the study year, 'minimum distance to spring oilseed rape in the previous season', 'edge density' and 'crop diversity' in generalised mixed effects models ('glmmTMB') including 'year' (factor, 5 levels) as random intercept (package GLMMTMB version 1.1.2.9000 Brooks et al., 2017). Separate models were fitted for each response and each of the three buffer radii. Field size was not correlated with any of the responses in initial analyses and thus not included in the models (Pearson's $|r| \le 0.16$). Similarly, we detected no significant or strong correlations between spring oilseed rape sowing date and any fixed effect at any radius (Pearson's $|r| \le 0.25$). All fixed effects were z-scaled to multiples of the standard deviation and mean centred

using the 'scale' command to improve model fits. There were no strong correlations (Pearson's $|r| \le 0.45$) or evidence for collinearity across all fixed effects (variance inflation factors ≤ 2.08 ; Johnston et al., 2018; Table S4). In models for flea beetle responses (count data), we used a negative binomial error distribution with 'log' link also accounting for overdispersion. In models for crop damage (proportion data), we used a beta regression with 'logit' link. All models for flea beetle responses contained 'trap days', that is the cumulative number of days of pitfall trapping in each sampling plot (log-transformed due to the selected residual distribution), as offset, to account for variation in sampling effort between fields. Additionally, using Pearson correlations between all flea beetle responses and cotyledon damage, we assessed whether the assumed positive relations were present.

All models were checked for under- and overdispersion, zero inflation and suitability of chosen residual distributions using the DHARMA package (version: 0.4.4 Hartig, 2022) and we detected no violation of the model assumptions. We tested model residuals with Mantel tests and detected no spatial autocorrelation in any of the models ($p \ge 0.313$). Model outputs were obtained using type II sums of squares Wald chi-square tests with the command 'Anova' (library 'car', version 3.0–12, Fox & Weisberg, 2019) and R^2 values with the command 'performance' (library 'performance', version 0.9.1, Lüdecke et al., 2021).

3 | RESULTS

Across all study sites, we collected 67,547 flea beetles belonging to 11 genera. Thereof, 49,196 belonged to the genus *Phyllotreta* (72.8%), 10,059 to the genus *Chaetocnema* (14.9%) and 8292 to the remaining nine genera (12.3%). Within the genus *Phyllotreta*, *P. atra* was the most common species with 15,470 individuals (22.9%), followed by *P. vittula* with 11,137 individuals (16.5%), *P. undulata* with 10,717 individuals (15.9%) and *P. striolata* with 10,432 individuals (15.4%; Table S3).

3.1 | Landscape effects on flea beetles

Overall, models at larger spatial scales explained comparable or larger shares of variance than models at the smaller spatial scale (Table S4). Forest cover was positively related to the densities of *P. undulata* at the 2000m radius, increasing densities by 2.2% per % forest cover increase, while this increase was only marginally significant at the 1000m radius (Figures 3 and 4a; Table S4). Pasture cover at the 2000m radius was positively related to the densities of *P. atra*, increasing densities by 1.2% per % pasture cover (Figures 3 and 4b; Table S4). Additionally, the densities of all *Phyllotreta* at the 2000m radius and the densities of *P. striolata* at the 500m radius marginally increased with pasture cover (Figure 3; Table S4). The distance to the nearest winter oilseed rape field in the study year was marginally negatively related to the densities of *P. undulata* at the 2000m radius (Figure 3; Table S4).



FIGURE 3 Model coefficients for forest cover, pasture cover, minimum distance to winter oilseed rape (WOSR) in the same year and spring oilseed rape (SOSR) in the previous year, edge density and Shannon crop diversity in the previous year in the three buffer radii 500, 1000 and 2000m for the responses: all flea beetles, all *Phyllotreta* sp., *P. atra*, *P. striolata*, *P. undulata*, *P. vittula*, *Chaetocnema* sp. and cotyledon damage with 95% confidence intervals. Fixed effects were scaled to magnitudes of the standard deviation (*z*-scaling), thus coefficients for flea beetles can be interpreted as changes in the response on the log scale per 1 standard deviation of the fixed effect. For cotyledon damage coefficients indicate changes in the log-odds ratio per 1 standard deviation of the fixed effect due to the logit link used in the models. (*) indicates p < 0.1, * p < 0.05, ** p < 0.01, *** p < 0.001. For statistics, see Table S4.

FIGURE 4 Selected statistically significant (*p* < 0.05) landscape effects with the largest effect sizes on flea beetle responses and cotyledon crop damage. All results are shown in Figure 3. The solid line is the model prediction for the radius stated in italics, the grey area is the 95% confidence interval. From top left to bottom right: the number of *P. undulata* in relation to forest cover (a), the number of *P. atra* in relation to pasture cover (b), the number of all *Phyllotreta sp.* (e), the number of *P. striolata* (f) as well as the percent of cotyledon damage (g) in relation to the distance to the nearest spring oilseed rape (SOSR) field in the previous year and the percent of cotyledon damage in relation to pasture cover (h). Numbers represent total catches but as the sampling effort between sites varied, models included offsets for the number of days the traps were active. As numbers of individuals varied strongly, four data points were omitted in the panels depicting *P. striolata* to improve graphical display. All data points can be seen in the logarithmic version of this figure in the Supporting Information (Figure S1). For statistics, see Table S4.





The distance to the nearest spring oilseed rape field in the previous year was consistently negatively related to all responses and throughout all spatial scales (Figures 3 and 4e,f; Table S4) except for *P. vittula* where densities only marginally decreased at the 2000 m

radius and for *P. atra* at the 2000m radius and *Chaetocnema* sp. where no predictor had effect. The density decrease varied from 11.0% (all flea beetles, 2000m radius) to 22.6% (*P. striolata*, 1000m radius) per 1000m.

Edge density was negatively related to densities of *P. striolata* at all scales but the decrease was strongest at the 500m radius with 5.7% per 1000m edge length (Figure 4d). Densities of *P. vittula* also decreased by 7.4% per 1000m edge length at the 500m radius (Figure 3; Table S4).

Landscape crop diversity in the previous year was positively related to the densities of all *Phyllotreta* (increase by 15.2% per 0.1 Shannon index increase), *P. undulata* (increase by 21.4% per 0.1 Shannon index increase) and *P. striolata* (increase by 18.0% per 0.1 Shannon index increase) at the 2000 m radius (Figures 3 and 4c; Table S4). Additionally, the densities of all flea beetles, *P. atra* and *P. vittula* marginally increased with landscape-level crop diversity at the 2000 m radius (Figure 3; Table S4).

3.2 | Landscape effect on cotyledon damage

All flea beetle responses were positively correlated with cotyledon damage (Pearson's $r: 0.39 \le r \le 0.67$; p < 0.003). There were no significant effects of forest cover, the distance to the nearest winter oilseed rape field, the crop diversity in the previous year or of edge density on cotyledon damage at any spatial scale.

Pasture cover at the 500 m scale was positively related to cotyledon damage, increasing cotyledon damage by 19.9% at 5% pasture, by 41.9% at 10% pasture and by 65.5% at 15% pasture compared with landscapes with no pasture (Figures 3 and 4h; Table S4). This relation was only marginally significant at the 1000 and 2000 m radii (Figure 3; Table S4). The distance to the nearest spring oilseed rape field in the previous year was negatively related to cotyledon damage at all three spatial scales, reducing cotyledon damage by 9.3% at a distance of 1000 m, by 41.8% at a distance of 5000 m and by 69.5% at a distance of 10,000 m to the nearest spring oilseed rape fields across the years (in the 500 m radius model; Figures 3 and 4g; Table S4).

4 | DISCUSSION

With a narrowing spectrum of available insecticides, approaches for insect pest regulation based on land use in the landscape gain importance. We show that aspects of both landscape composition and configuration affect flea beetles and crop damage in spring oilseed rape. We found no apparent 'one-fits-all' solution for pest control in landscape planning. The effects of non-crop habitat cover, edge density and crop diversity varied depending on pest species and landscape scale considered, likely due to differences in pest ecology and life cycles. Tailoring landscapes towards specific economically relevant pests thus requires differentiated approaches. However, isolation from spring oilseed rape fields in the previous year consistently decreased pest densities and crop damage.

4.1 | Variable effects of non-crop habitats

Limiting the availability of overwintering habitat is one possibility for landscape-level pest regulation. *P. undulata* was positively related to

forest cover at the 2000m radius scale. P. atra and, marginally, also P. striolata were positively related to pasture cover at the 500 m and 2000m radius scales, respectively. Differences in preferred overwintering habitats among Phyllotreta species (Burgess, 1981; Ulmer & Dosdall, 2006) could explain the species-specific responses to non-crop habitats. Hence, the role of non-crop habitats and their scale of effect for pests are not easily generalisable and depend on species-specific habitat preferences, even among closely related flea beetle species. This makes landscape scale planning difficult as it needs to be aligned with the ecology of target pest species that is not sufficiently studied for many species, and consider potential negative effects on natural enemies that might benefit from the same non-crop habitats (Martin et al., 2019; Tscharntke et al., 2016). While natural enemies and parasitism rates of flea beetles have partly been mapped (Ekbom, 1991; Ekbom et al., 2014), top-down control of flea beetles and its interactions with landscape structure require further exploration. Overall, the suitability of altering noncrop habitat cover as a means to control flea beetles in spring oilseed rape appears limited.

4.2 | Strong distance decay effects of oilseed rape in the previous year

For overwintering, flea beetles likely chose non-crop habitats in close proximity to their host crop fields (Zheng et al., 2020). Additionally, they also overwinter directly in the soil of harvested oilseed rape fields (Burgess, 1981). The isolation from host crop fields in the previous season could thus determine the colonisation of host crop fields in the following season. We indeed found the distance to the closest spring oilseed rape field in the previous season to be the strongest predictor across responses and spatial scales, being negatively related to the densities of all flea beetles except *Chaetocnema sp.* Moreover, the distance to the closest spring oilseed rape field in the previous season was, apart from pasture cover, the only landscape-level factor affecting crop damage.

Based on the relation between spring oilseed rape yield and cotyledon damage (Lundin, 2020) and the mean market prices for spring oilseed rape from 2016 to 2020 (Swedish Rural Economy and Agricultural Societies, 2021), increasing the distance from 0 to 5000 m to the closest spring oilseed rape field in the previous year would increase yields on average by 277.1 to 313.3 kg per ha and result in a monetary gain of 98.1 to 110.9 Euro per ha according to our model predictions (depending on the spatial scale at which land-use was measured). Our results indicate that the isolation of newly established spring oilseed rape fields from fields sown with the same crop in the previous year is the most promising strategy to reduce pest densities (thereby also the need for pesticides) and prevent crop damage. Similar spatiotemporal legacy effects have been shown for several other pest species and crops (e.g. Hederström et al., 2022 or Huusela-Veistola & Jauhiainen, 2006). Distance decay effects of pest dispersal between growing seasons are thus likely a general phenomenon that could be used for

regulation of host specialised pest species. While distance decay effects could also be assumed for top-down control by specialised parasitoids, parasitisation remained stable independent of distance to the host crop in the previous season in a recent assessment in winter oilseed rape (Sulg et al., 2023).

We, however, found no evidence that winter oilseed rape fields (or their direct surroundings) that could have been colonised in the cotyledon stage in early autumn served as overwintering sites. This is likely due to a phenological asynchrony of winter oilseed rape and the flea beetle pests of spring oilseed rape that are spring breeders and likely do not benefit from winter oilseed rape during its cotyledon stage in autumn.

4.3 | Limited effects of edge density and crop diversity

Edge density can benefit natural enemy populations and natural pest control (Martin et al., 2019), probably because crop field edges maintain a high natural enemy richness and buffer assemblage shifts caused by field management across years (Boetzl et al., 2020). We found negative relations between edge density and flea beetle densities only for P. striolata and P. vittula. However, because we found no positive effects of edge density on flea beetle densities, the importance of edges as overwintering habitat for flea beetles is either low or reduced by simultaneous benefits for natural enemies. Based on our results, smaller patch and field sizes, that is a more fine grained landscape, especially in the direct surroundings of spring oilseed rape fields, should be beneficial for flea beetle regulation. However, this effect was limited to two species. P. striolata and P. vittula, and not reflected in crop damage. In our study area, where non-crop habitats are generally abundant, edge density is likely less important for pest regulation in spring oilseed rape compared with other factors.

Crop diversity in the landscape can benefit natural pest control, probably as more resources are provided to natural enemies in more diverse landscapes (Redlich et al., 2018). Hence, we assumed flea beetle densities and crop damage to be negatively related with increasing crop diversity. However, we found the opposite for *P. undulata* and *P. striolata* and for all *Phyllotreta sp.* at the 2000m scale, with trends also for *P. atra* and *P. vittula*. Although the drivers of this effect remain unknown as no specific crop type was strongly correlated with crop diversity at this scale (Pearson's $|r| \le 0.30$), increased crop diversity might provide more resources also for insect pests and is apparently not universally positive for pest control.

5 | CONCLUSIONS

Our results show that considering landscape context and planning crop production accordingly can reduce densities of several flea beetle species and crop damage in spring oilseed rape. Especially spatial

isolation from host crop fields in the previous year is an important and plannable factor. Additionally, increasing edge density by reducing field sizes can decrease the abundance of some flea beetle species. More generally, limiting landscape host crop availability in the previous year emerges as an important factor for reducing pest pressure for multiple insect pests (Delaune et al., 2021). However, the strategic planning of agricultural landscapes for pest control often goes beyond the individual farm level and requires an integration of multiple land- and stakeholders to avoid spatial mismatches and ensure the expected benefits (Lundin et al., 2021). Our results also highlight the need to tailor strategies to the ecology of target pest species that react to contrasting aspects of the landscape context based on their ecology and life history. Landscape-scale pest control approaches hence require an improved understanding of pest ecology, life cycles and their interactions with natural enemies. While there may not be a convenient 'one-fits-all' approach for designing landscapes for pest control, our results clearly indicate that focusing strategies on certain aspects of landscapes important for specific pests at meaningful scales holds great potential for a sustainable and less pesticide-reliant crop production.

AUTHOR CONTRIBUTIONS

Ola Lundin and Riccardo Bommarco designed the study and coordinated the fieldwork, Guillermo Aguilera extracted the landscape information, Fabian A. Boetzl analysed the data and wrote the first draft of the manuscript. All authors interpreted the results, revised the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Swedish University of Agricultural Sciences Archive: https://hdl.handle.net/20.500.12703/4015 (Boetzl et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Selected statistically significant (p < 0.05) landscape level effects on different flea beetle responses and cotyledon crop damage. The solid line represents prediction from the model for the radius stated in italics, the grey area represents the 95% confidence interval. From top left to bottom right: the number of *P. undulata* in relation to forest cover at the 2000m scale (A), the number of *P. atra* in relation to pasture cover at the 2000m scale (B), the number of *P. undulata* in relation to Shannon crop diversity at the 2000m scale (C), the number of *P. striolata* in relation to edge density at the 1000m scale (D) and the number of all *Phyllotreta sp.* (E), the number of *P. striolata* (F) as well as the percent of cotyledon damage (G) in relation

to the distance to the nearest spring oilseed rape (SOSR) field in the previous year at the 1000 and 500m scales, and the percent of cotyledon damage in relation to pasture cover at the 500m scale (H). Numbers represent total catches but as the sampling effort between sites varied, models included offsets for the number of days the traps were active. Response axes are logarithmic. For statistics, see Figure 3 and Table S4.

Table S1. The 14 crop classes used to calculate Shannon crop diversity in all three buffer radii with the number of landscapes in which the respective classes were present, their total area (in hectares) and the proportion of the buffer area covered (in percent). The class 'other' refers to green fodder and manure crops, other horticultural crops or other crops not categorised in the crop database of the Swedish Board of Agriculture. Values rounded to two digits.

Table S2. Mean, standard error and range for landscape characteristics at 500, 1000 and 2000m scales. Values rounded to the number of decimals in the original data, crop diversity and percentages rounded to two decimals, edge density rounded to decimetres.

Table S3. Flea beetle (Coleoptera, Alticini) species caught throughout the 5 years and in total (total numbers for each year as well as percent rounded to one digit). Blanks indicate that no individuals were caught for the respective species and year. The number of fields differed between the years and is stated in brackets behind the year.

Table S4. Variance inflation factors (VIF) and model results for the three different buffer radii for all eight responses against the five fixed effects (i) the cover of forest (proportion), (ii) the cover of pastures (proportion), (iii) the distance to the closest winter oilseed rape (WOSR) field in the study year, (iv) the distance to the closest spring oilseed rape (SOSR) field in the previous year, (v) edge density and (vi) Shannon crop diversity in the previous year. Coefficients are standardised as multiples of the standard deviation (SD) of the response ('z-scoring'); Cl=confidence interval; *df*=degree of freedom (numerator, denominator); χ^2 =chi-square value obtained from Wald type II chi-square tests; *p*=*p*-value; R^2_m =marginal R^2 ; R^2_c =conditional R^2 .

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