Sharing the burden: Cabbage stem flea beetle pest pressure and crop damage are lower in rapeseed fields surrounded by other rapeseed crops

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Abstract

The cabbage stem flea beetle (*Psylliodes chrysocephala*) is a significant pest of rapeseed (*Brassica napus*). Feeding by adult *P. chrysocephala* can cause severe leaf damage and larval infestation can reduce stem strength, both of which impact crop growth and development, causing substantial yield losses and economic damage. The structure of the agricultural landscape can regulate herbivorous pest populations through top-down and bottom-up processes. This has shown promise in regulating the populations of other herbivorous pests, but remains relatively unexplored for *P. chrysocephala.* Here we investigate how the structure of the agricultural landscape influences *P. chrysocephala* abundance (pest pressure) and associated crop damage. We also examine the effect of the landscape on natural enemies and their ability to regulate *P. chrysocephala* populations. We show that *P. chrysocephala* populations are primarily regulated through bottom-up processes. We identify adjacency to another rapeseed crop and the total proportion of rapeseed grown in the landscape as key factors influencing beetle pressure, crop damage, and larval infestation, but find no effect of host crop proportions grown in the previous year at the examined scales up to 1 km surrounding focal crops. We also observe positive effects of crop heterogeneity and semi-natural habitat proportions on natural enemy abundance and diversity; however, these increases had no direct impact on *P. chrysocephala*. Bottom-up processes appear to contribute to herbivorous pest regulation by diluting beetles in the landscape, and could represent an important mechanism for sustainably managing pest populations by adapting the proportions and neighbourhoods of rapeseed crops at small to large spatial scales.

Keywords

Herbivorous pest; Pest suppression; Pest regulation; *Psylliodes chrysocephala.*

1. Introduction

Rapeseed, *Brassica napus,* is one of the most widely cultivated oilseed crops (Carré and Pouzet, 2014). Rapeseed confers myriad benefits to agricultural systems; for example, rapeseed acts as an economically attractive break crop in crop rotations and supports a diverse ecological habitat (Alford, 2000; Forleo et al., 2018; Kirkegaard et al., 1993). Rapeseed can be attacked by a range of herbivorous pests that inflict crop damage (Alford et al., 2003; Edde, 2021; Zheng et al., 2020). Of these, the cabbage stem flea beetle, *Psylliodes chrysocephala,* is of significant importance (Edde, 2021; Tixeront et al., 2023), having been recently ranked as the top biotic threat facing European rapeseed production (Zheng et al., 2020)*. P. chrysocephala* adults damage plants through leaf feeding between July and October, causing up to 25% yield loss (Conrad et al., 2021; Edde, 2021; Ferguson et al., 2003). The larvae also cause significant damage between October and February when they burrow into the plant stem, with high infestation delaying crop maturation with strong impacts on yields (Conrad et al., 2021; Edde, 2021; Ortega-Ramos et al., 2022b).

Until recently, *P. chrysocephala* were primarily controlled using neonicotinoid seed treatments (Ortega-Ramos et al., 2022a), but restrictions on neonicotinoids have increased *P. chrysocephala* risk for rapeseed growers (Ortega-Ramos et al., 2023). Currently, pyrethroids are the only alternative chemical control option. However, overuse of pyrethroids has led to the development of insecticide resistance (Højland et al., 2016; Willis et al., 2020). In turn, this has increased the need for more sustainable non-chemical management practices (Ortega-Ramos et al., 2022a). In-field strategies for sustainable management include the integration of companion crops, sowing into straw mulch (Seimandi-Corda et al., 2023), and intercropping with legumes (Breitenmoser et al., 2022). However, the effectiveness of these methods can vary seasonally (Breitenmoser et al., 2022; Seimandi-Corda et al., 2023).

Herbivorous pests can also be influenced by the composition and configuration of the agricultural landscape (Delaune et al., 2021; Haan et al., 2020; Marini et al., 2023; Martin et al., 2019; Veres et al., 2013; Zhang et al., 2020). Generally, the agricultural landscape can influence herbivorous pests through two mechanisms: top-down (e.g., by encouraging the presence, diversity, and activity of natural enemies of pests, including predators and parasitoids) and bottom-up (e.g., by manipulating the proportion of host crop habitat and overwintering sites of the pests; Han et al. (2022)). Limiting resource (host crop) availability can interrupt insect reproduction and migration cycles, which can have significant impacts on the populations of specialist herbivores.

Successful top-down suppression is dependent on the presence and effectiveness of natural enemies (Dainese et al., 2017), themselves reliant on the availability of habitats and other resources, including non-cropped or seminatural habitats (Martin et al., 2019). In order to encourage top-down suppression of herbivorous pests, knowledge of the natural enemy communities likely to suppress them is needed. Only a few natural enemies of *P. chrysocephala* have been described (Hoarau et al., 2022). The level of successful control varies greatly (Hoarau et al., 2022), with the Ichneumonid wasp, *Tersilochus tripartitus,* showing the greatest biocontrol potential (Alford, 2000). For predators, field observations have identified spatial associations between two Carabid beetles (*Trechus quadristriatus* and *Pterostichus madidus*) and *P. chrysocephala* larvae (Warner et al., 2003), indicating that some carabid species might prey on *P. chrysocephala*. It has been proposed that generalist natural enemies of other flea beetles might also prey on *P. chrysocephala* (Hoarau et al., 2022), although there is no direct evidence of this. Generally, higher natural enemy abundance and diversity leads to increased pest suppression (Dainese et al., 2019; Dainese et al., 2017), and supporting natural enemy communities presents an avenue for sustainable management.

Bottom-up approaches involve manipulating habitat availability (proportion of host crops) or crop heterogeneity (the diversity of crops) in a landscape to decrease the density and population pressure of herbivorous pests by limiting resources (Almdal and Costamagna, 2023; Boetzl et al., 2023). Bottom-up approaches have been described to contribute towards herbivorous pest regulation in similar crop-beetle systems (Boetzl et al., 2023; Zavalnitskaya et al., 2022), and could potentially be used for the sustainable management of *P. chrysocephala*. One variable that is relatively easy to manipulate is the proportion of host crop in the landscape; indeed, increased host crop proportion within the growing season has been shown to decrease the abundance of several other herbivorous pests of rapeseed, including pollen beetle, stem weevil, and brassica pod midge (Rusch et al., 2013; Thies and Tscharntke, 1999; Zaller et al., 2008a; Zaller et al., 2008b). Furthermore, proximity to a host crop grown in the previous year can influence herbivorous pest pressure and crop damage, due to these fields acting as a source for insect populations in the following year (Boetzl et al., 2023; Sulg et al., 2023). Similarly, the heterogeneity of crops planted across the landscape in previous and current years can also influence herbivorous pest pressure and damage (Akter et al., 2023; Almdal and Costamagna, 2023; Scheiner and Martin, 2020; Veres et al., 2013). However, it is not known how these bottom-up processes impact *P. chrysocephala* pressure and associated crop damage.

These landscape effects are in-line with the landscape-moderated concentration and dilution hypothesis (Tscharntke et al., 2012). Higher host crop proportions in the previous compared to the current year could provide resources to support large herbivorous pest populations, which may immigrate in high numbers (concentration) into fields in the following year. This has recently been reported for *P. chrysocephala*, with fields within 0-2 km of a previous crop having a higher probability of experiencing damage than fields that are further away (Hausmann et al., 2023). In contrast, if host crop proportions are higher in the cropping year than the previous year, this may facilitate the dispersal of insects across the landscape and lead to lower densities (dilution) in individual fields (Zavalnitskaya et al., 2022). However, these effects tend to vary considerably between herbivore species (Boetzl *et al.* 2023) and are likely to depend strongly on the spatial scale of consideration. The concentration and dilution effect is thought to impact habitat specialists with a smaller host range, such as *P. chrysocephala* (Williams, 2010), more than generalists (Tscharntke et al., 2012). As different aspects of agricultural landscapes contribute towards bottom-up and top-down insect control, land-use planning at the landscape scale could be used to develop sustainable insect management strategies (Lundin et al., 2021).

Here, we seek to elucidate how the agricultural landscape affects *P. chrysocephala* pressure and crop damage in rapeseed. To achieve this, we characterised the landscape surrounding 14 rapeseed fields, monitored the local arthropod community in each field, and recorded *P. chrysocephala* pressure, leaf damage, and larval infestation. We hypothesize that (Fig. 1): 1) Host crop proportion will have a concentration-and-dilution effect on beetle pressure, with greater host crop proportions in the cropping year decreasing beetle pressure; 2) Adjacency to another rapeseed field in the cropping year will reduce beetle pressure by dispersing insects locally; 3) Fields in close proximity to previous year rapeseed fields will suffer from higher beetle pressure; 4) Greater proportions of seminatural habitat and crop heterogeneity provide increased refugia and resources to support higher natural enemy abundance and diversity, whereas greater crop heterogeneity provides more refuge habitat for migrating beetles; 5) Higher natural enemy abundance and diversity will negatively affect beetle pressure and associated crop damage via the provision of increased pest suppression services. Our work provides insight into the top-down and bottom-up effects of the landscape on herbivorous pests and highlights the potential applications for landscape-driven suppression of an important herbivorous pest in an agriculturally relevant cropping system.

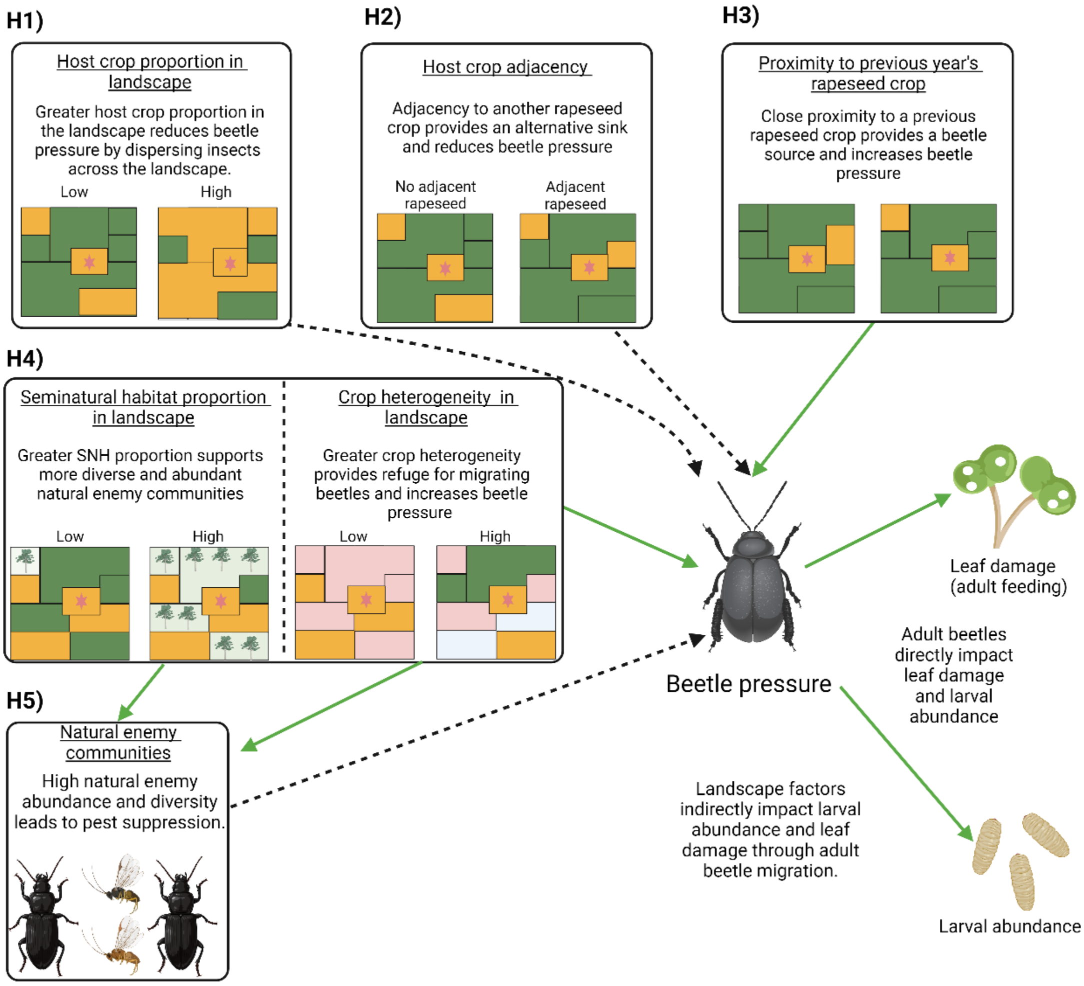

Fig. 1: Graphical representation of proposed interactions between *P. chrysocephala* and the landscape. Green arrows (solid) indicate positive effects and black arrows (dashed) indicate negative effects. In the landscape diagrams: Orange squares denote rapeseed fields; pale blue, pink, and green squares represent other crop types; semi-natural habitats (SNH) are represented by pale green squares containing tress; red star indicates the location of the focal field. Image was compiled in bioRender.

2. Materials & Methods

2.1 Site selection and landscape characterisation

Fourteen winter rapeseed fields were selected across a landscape gradient (proportion of agricultural land in the landscape). Crops were sown in late August or early September 2021, fields were drilled and managed by the host farmer (see Table S1 for agronomic information for each field) and located in a key rapeseed production region in Lower Saxony, Germany (Fig. 2). The landscape around each field was characterised at three spatial scales: 500 m, 750 m and 1 km radii. To ensure independence of the landscapes surrounding the sites, we selected the sites to be a minimum distance of 1 km apart (the two closest sites were 1.1 km apart). We also noted whether each field neighboured another winter rapeseed field.

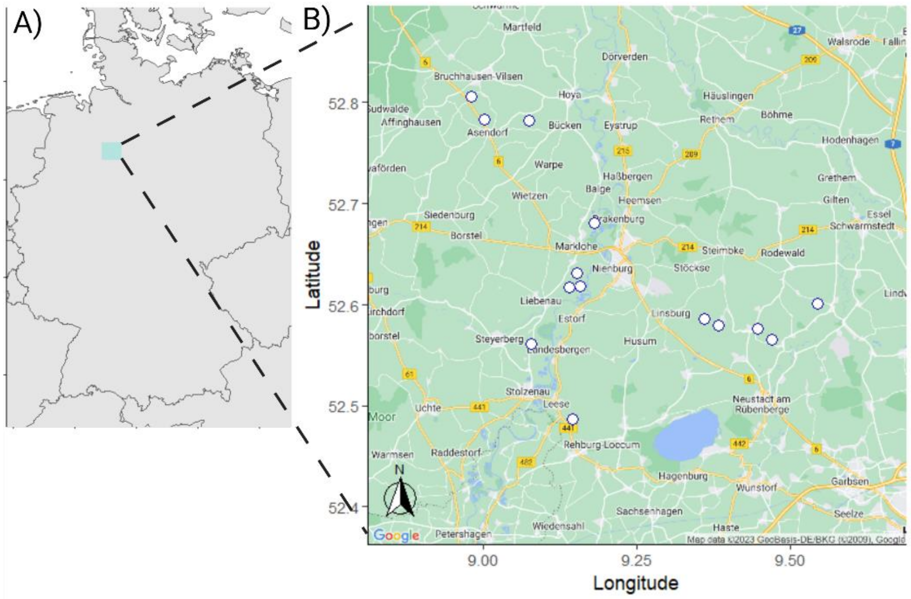

Fig. 2: A) Location of the study region in Germany (blue shaded area) and B) location of the 14 rapeseed fields (white circles). Maps were created in ggmap (v.3.0.2) with the base map used in B) obtained from Google Map Services. Image was compiled in bioRender.

We characterised the agricultural landscapes using open-access digital crop-cover maps. Detailed crop maps were obtained from the Lower Saxony federal database on agricultural development (Servicezentrum Landentwicklung und Agrarförderung). These geodata contain information on crop species grown in each field across Lower Saxony and are updated annually. We calculated the proportion of rapeseed crops in each radius. We assessed the compositional heterogeneity of crops (hereafter crop heterogeneity) by extracting the total number of fields for each crop species present in the landscape, and calculating Shannon's Diversity Index. Table S2 details the number of crop types included at each spatial scale for each year. We retrieved data on semi-natural habitat from the Lower Saxony ATKIS database (ATKIS-Objektartenkatalog), this database comprises a digital land-use cover map and we calculated seminatural habitat by summing the total proportion for forest, woodland, heath, moor, swamp, and uncultivated land.

We considered the following landscape variables at each spatial scale surrounding focal rapeseed fields: The proportion of rapeseed fields planted in the previous cropping season, the proportion of rapeseed fields planted in the cropping season, crop heterogeneity in the previous cropping season, crop heterogeneity in the cropping season, the change in rapeseed growing area between years, and the proportion of seminatural habitat in the cropping year. We carried out landscape characterisation using QGIS v.3.24.3 and tested for correlations between each landscape variable (Fig. S1-S3). Change in rapeseed proportion and rapeseed proportion in the previous year were colinear at all spatial scales (Fig. S1-3; cor 0.794 – 0.863) so we discarded change in rapeseed proportion from downstream analysis. We used Moran's I test to assess the spatial autocorrelation of the remaining landscape variables. Spatial autocorrelation analysis indicates that only one variable (previous year crop heterogeneity at the 500 m spatial scale) was spatially autocorrelated, no autocorrelation was detected for any other landscape variable (Table S3; Fig. S4-S6).

2.2 Experimental design and field assessments

Each field comprised two 100 m long transects with five 2 m^2 quadrats spaced equidistantly along the transect. Both transects ran parallel to the field edge, the first transect was 5 m from the field boundary and the second transect was 25 m from the field boundary. Insect traps were placed at the central quadrat along each transect.

2.2.1 Assessments and sampling

Fields were visited weekly for five weeks from w/c 27.09.2021 until w/c 25.10.2021, coinciding with the main period of *P. chrysocephala* migration (Conrad et al., 2021), and were used to determine pest pressure. Pest pressure was measured by installing a yellow pan trap at vegetation height in the central quadrat along each transect. Traps were exposed for seven days and the number of beetles caught was used to determine weekly pest pressure.

Three rounds of in-crop assessments were carried out in September (w/c 27.09.2021; calendar week 39), October (w/c 25.10.2021; calendar week 43), and November (w/c 22.11.2021; calendar week 47). In-crop assessments comprised two adult feeding damage assessments (September and October), a larval abundance assessment (November), and invertebrate trapping (September, October, and November). Timing of these assessments corresponded with peak periods of *P. chrysocephala* migration (September), egg laying (October), and the early periods of larval infestation (October/November) (Conrad et al., 2021).

For the leaf damage assessments, the proportion of leaf-area eaten was scored for 20 random plants per quadrat in September and October. *P. chrysocephala* damage can be distinguished from other damage (e.g., slug damage) by the characteristic shot-holes produced during feeding. The larvae abundance assessment consisted of randomly selecting five plants per quadrat, the diameter of the stem of each plant was recorded and the plant was dissected. Any *P. chrysocephala* larvae present in each stem were grouped by instar stage and the total larvae number was recorded.

Invertebrate trapping involved installing a pair of invertebrate traps (a yellow pan trap and a pitfall trap) in the central quadrat of each transect. Each trap was 1/3 full of water with a few drops of detergent. Pan traps were exposed for 48 h and pitfall traps for one-week. Pan traps were uncovered and placed within the crop canopy, pitfall traps were installed flush with the soil surface and covered with a rain roof. Trap contents were collected in 70% ethanol, and stored in glass jars until analysis. The total abundance of invertebrates was recorded and individuals were grouped into Order. Family-level identification was carried out for the Coleoptera, Hymenoptera, and Aranea. We used Schaefer (2018) to support invertebrate identification. As relatively little is known about the natural enemies of *P. chrysocephala* we used a proxy measurement for natural enemies that comprised arthropod groups previously described to contain natural enemies of *P. chrysocephala* as well as more generalist predator groups: Braconidae, Ichneumonidae (Hymenoptera); Caribidae (Coleoptera); Dysderidea, Theridiidae, Linyphiidae, Thomisidae, Lycosidae, Opiliones (Aranea). We calculated natural enemy α-diversity using Shannon’s diversity metric.

We were not able to obtain yield data from the study sites as a high number of fields suffered from crop failure in the spring following infestation with cabbage root fly (*Delia radicum).*

However, we believe that our study provides important insight into the landscape drivers behind *P. chrysocephala* risk and subsequent crop damage. Leaf damage at the cotyledon stage can be a useful proxy for potential yield-reducing damage as correlations between flea-beetle damage and yield loss have been described in spring rapeseed (Lundin, 2020).

2.3 Statistical analysis

Data were analysed in R Studio v.2022.02.3 running R (Ihaka and Gentleman, 1996) v.4.20. The following additional packages were used for data pre-processing: tidyverse (v.1.3.1; Wickham et al., 2019); data analysis: ape (5.7-1; Paradis et al., 2019), car (v.3.1-0; Fox and Weisberg, 2018), DHARMa (v.0.4.6; Hartig and Lohse, 2017), glmmTMB (v.1.1.7; Brooks et al., 2017), vegan (v.2.6-2; Dixon, 2003), lme4 (v.1.1-34; Bates et al., 2014), MuMIn (v.1.47.1; Barton, 2009), piecewiseSEM (v.2.3.0; Lefcheck, 2016); data visualisation: ggplot2 (v.3.3.6; Wickham, 2016), ggpubr (v.0.4.0; Kassambara, 2020), GGally (v.2.1.2; Schloerke et al., 2021), ggmap (v.3.0.2; Kahle et al., 2013).

We analysed the response variables beetle pressure, larvae abundance, and natural enemy abundance using generalised linear mixed models with negative binomial distribution in R package glmmTMB (Brooks et al., 2017). The response variables leaf damage and Shannon diversity of natural enemies were modelled using linear mixed effects models in R package lme4 (Bates et al., 2014). In all models, we included field as a random factor in order to account for variation in agronomic practices (e.g., planting scheme, crop management etc.) and for multiple sampling within each field. We used a Variance Inflation Factor (VIF) cut-off value of five to define collinear variables (Zuur et al., 2009) and removed any explanatory variables that breached this threshold. All other non-colinear explanatory variables were retained in the final model and final models were tested for significance using analysis of deviance tests (Type II Wald X^2 tests). The fitted-residual plots of the final models were assessed to check model suitability and conformance to model assumptions.

2.3.1 Data pooling and transformations

To avoid zero-inflation, leaf damage data were averaged at the quadrat level and the total number of larvae was summed at the quadrat level. Natural enemy abundances were summed and natural enemy family richness was pooled across the two trap types. We calculated two beetle pressure metrics: Beetle pressure at week 39 and cumulative beetle pressure (sum of all beetle numbers from week 39-43). This produced 56 observations for beetle pressure, 280 for feeding damage, 140 for larvae abundance, and 84 for natural enemies. Leaf damage data were logit transformed to account for bound proportional data (Warton and Hui, 2011). To aid model convergence the proximity to previous year rapeseed was square-root transformed. These transformed data were used in all analyses described below.

2.3.2 Data analysis

To determine how beetle pressure influenced leaf damage and larvae abundance we modelled leaf damage observed during the first assessment round against beetle pressure in week 39, and leaf damage observed during the second assessment round and larvae abundance against cumulative beetle pressure.

To test the influence of neighbouring rapeseed crops, we modelled cumulative beetle pressure, leaf damage, and larvae abundance against adjacent rapeseed field, proximity to a rapeseed crop in the previous year, the total abundance of natural enemies, and α-diversity of natural enemies. Natural enemy abundance and diversity were not correlated (r = 0.136; t = 1.24; df = 82; p = 0.217).

We examined the influence of the landscape on beetle pressure, leaf damage, larvae abundance, natural enemy abundance, and natural enemy α-diversity in three separate models, one for each spatial scale (500, 750, and 1,500 m radii). In all models, explanatory variables included the calculated landscape variables (detailed in Section 2.1 above). In models explaining beetle pressure, leaf damage, and natural enemy abundance and diversity, assessment round was included as an explanatory variable. Where multiple spatial scales were found to influence the response variable, we used Akaike Information Criterion values corrected for small sample sizes (AICc) to identify the spatial scale that best explained the observed variation. To achieve this, we considered models with lower AICc values as better predictors of the response variable (Burnham and Anderson, 2002; Moraga et al., 2019). When comparing AICc values, we used ΔAICc >2 to indicate difference in model fit.

2.3.3 Piecewise structural equation modelling

We used piecewise structural equation modelling (Lefcheck, 2016) to further explore the direct and indirect effects of the landscape. For this, we built models that only contained variables identified as significant in our prior analyses; each model included field as a random effect. We extracted standardised coefficients and evaluated model fit using Fisher's C statistic.

3. Results

3.1. Do **P. chrysocephala** *pressure, rapeseed adjacency, and natural enemies influence leaf damage and larval load?*

Adult beetle pressure observed at the start of the monitoring period was positively related to the leaf damage observed in the same week (calendar week 39; $X^2_1 = 37.43$; p = <0.001; Fig. 3A; Table S4). We observed a similar positive relationship between cumulative beetle pressure and leaf damage during the second assessment round in late October (calendar week 43; $X^2_1 = 7.79$; p = 0.005; Fig. 3B; Table S4). Cumulative beetle pressure also positively influenced larvae abundance in November ($X^2_1 = 52.81$; p = <0.001; Fig. 3C; Table S4). Furthermore, the presence of a rapeseed field adjacent to the focal rapeseed crop significantly decreased beetle pressure ($X^2_1 = 15.89$; p = <0.001; Fig. 3D), leaf damage ($X^2_1 = 7.65$; p = 0.006; Fig. 3E), and larvae abundance in the focal field ($X^2_1 = 6.52$; p = 0.011; Fig. 3F). Proximity to the nearest rapeseed crop grown in the previous year did not affect beetle pressure, leaf damage, or larvae abundance (Table S5).

In contrast, we did not detect any significant influence of the abundance and diversity of natural enemy communities on beetle pressure, leaf damage, or larvae abundance (Table S6). However, because little is known about antagonists of *P. chrysocephala* the natural enemy groups examined here (Braconid and Ichneumonid wasps, Carabid beetles, and spiders) can only be considered as potential enemies of *P. chrysocephala*.

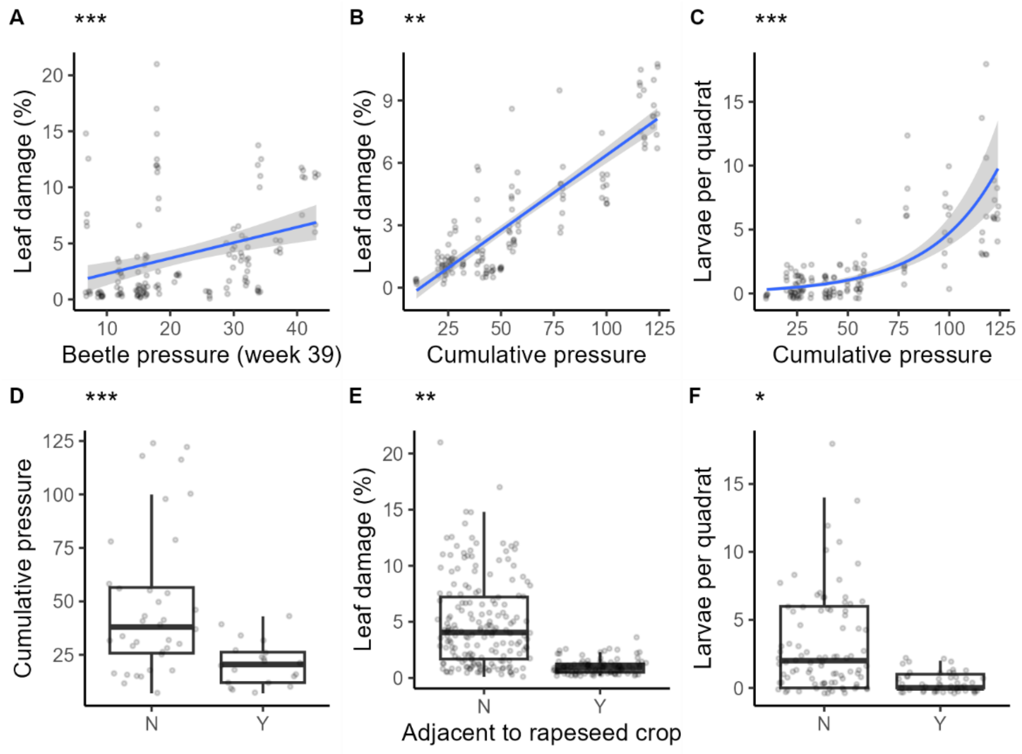

Fig. 3: A) The relationship between the beetle pressure observed in week 39 and the mean percent of leaf damage observed during assessment round one; B) The relationship between cumulative beetle pressure over all five weeks (week 39-43) of monitoring and the mean percent of leaf-area damage observed during assessment round two; C) The relationship between cumulative beetle pressure and mean larvae abundance during assessment round three. Blue lines show predicted values of the models. Shaded areas represent the confidence intervals. D-F) The influence of an adjacent rapeseed crop on cumulative beetle pressure (D), mean percent of leaf damage (E), and total larvae abundance (F). Underlying data are displayed as grey points. Asterix denotes level of significance for associated statistical tests: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

3.2 P. chrysocephala ***pressure and crop damage are affected by the proportion of winter rapeseed***

We examined how the agricultural landscape affects beetle pressure, leaf damage, and larvae abundance at three spatial scales (500 m, 750 m, and 1 km radii). We observed significant effects of the proportion of rapeseed in the cropping year on beetle pressure and leaf damage at the 500 m radius (Fig. 4; Table S7; Table S8): Beetle abundance ($X^2_1 = 4.66$; $p = 0.031$; Fig. 4A) and leaf damage ($X^2_1 = 4.99$; $p = 0.026$ Fig. 4B) were lower at sites with a higher rapeseed proportion. No other tested landscape variable or spatial scale affected beetle pressure or leaf damage.

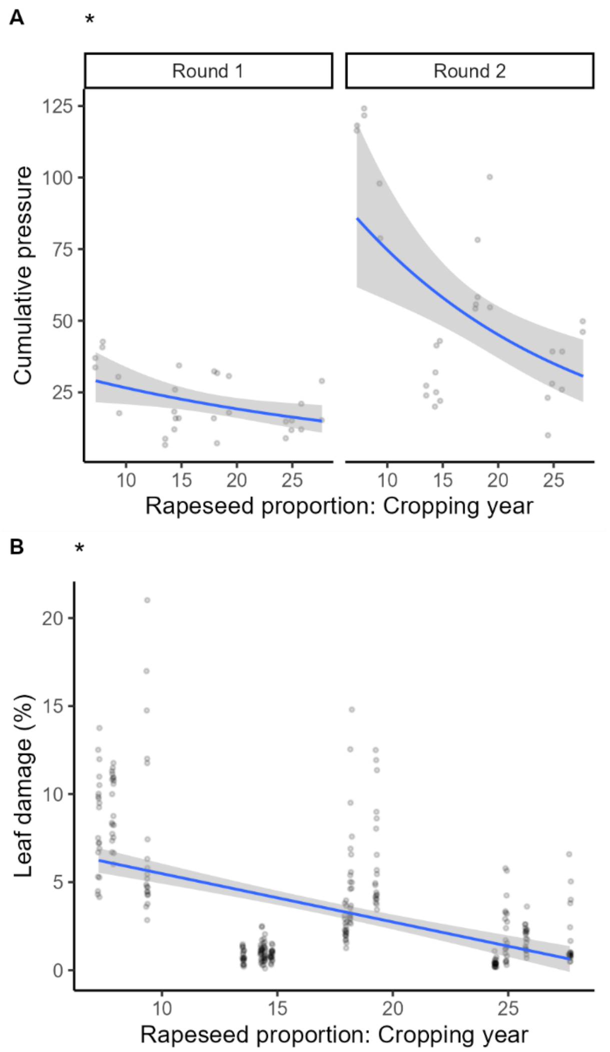

Fig. 4: Relationship between cumulative beetle pressure, leaf damage, and the agricultural landscape at the 500 m spatial scale. Influence of rapeseed proportion in the cropping year on: A) Cumulative beetle pressure; B) Leaf damage (%). Lines in panel A show the general linear regression and lines in panels B show the linear regression; shaded areas represent the confidence intervals. Underlying data are displayed as grey points. Panel A shows data separately for each assessment round. Asterix denotes level of significance for associated statistical tests: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Larvae abundance was influenced by host crop proportion in the cropping year and previous year crop heterogeneity (Table S9). Fewer larvae were observed as the proportion of winter rapeseed grown in the cropping year increased at a 500 m spatial scale ($X^2_1 = 9.62$; $p = 0.002$; Fig. 5A) and higher larvae abundance was observed at sites with a greater previous year crop heterogeneity ($X^2_1 = 7.24$; $p = 0.007$; Fig. 5B). No other landscape variable or spatial scale influenced larvae abundance (Table S9).

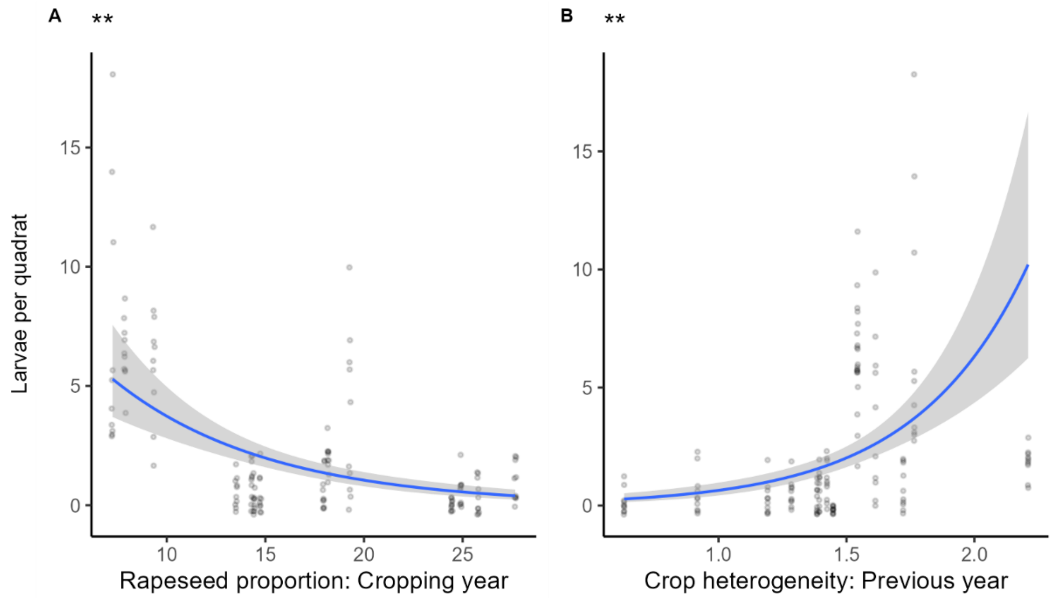

Fig. 5: Relationship between larvae abundance and the agricultural landscape at the 500 m spatial scale. A) Influence of rapeseed proportion in the cropping year; B) Crop heterogeneity in the previous year. Lines show the general linear regression; shaded area represents the standard error. Underlying data are displayed as grey points. Asterix denotes level of significance for associated statistical tests: * p < 0.05; ** p <0.01; *** p <0.001

3.3 Landscape effects on natural enemy communities

Natural enemy abundance was influenced by several landscape variables at all spatial scales. Natural enemy abundance was higher in fields with a greater crop heterogeneity in the previous ($X^2_1 = 6.42$; $p = 0.011$; Table S10; Fig. S7A) and cropping year ($X^2_1 = 6.35$; $p = 0.012$; Table S10; Fig. S7B) at the 500 m spatial scale. Natural enemy abundance was also affected by cropping year crop heterogeneity and the proportion of seminatural habitat in the landscape at the 750 and 1,000m spatial scales (Table S10; Fig. S7). The α-diversity of the natural enemy communities increased as rapeseed proportion increased in the previous year at the 1,000 m spatial scale (Table S11; Fig. S8).

3.4 Structural equation modelling

Beetle pressure influenced leaf damage and larvae abundance, and all three decreased when the experimental field was adjacent to another rapeseed field (Fig. 3). Two landscape parameters were identified as important drivers of beetle pressure, leaf damage, and larvae abundance: An increasing proportion of rapeseed in the landscape in the cropping year reduced beetle pressure, leaf damage, and larvae abundance (Fig. 4; 5); larvae abundance was higher in fields with a greater crop heterogeneity in the previous year (Fig. 5). We constructed a piecewise structural equation model to identify the potential cascading effects between these bottom-up variables, focussing on the 500 m spatial scale (Fig. 6). Natural enemy communities were also affected by several bottom-up landscape parameters (Fig. S7, S8) but had no direct influence on beetle pressure or associated crop damage. For clarity, natural enemies were not included in Fig. 6.

The piecewise structural equation model indicated that beetle pressure was strongly influenced by the proportion of rapeseed grown in the cropping year and adjacency to another rapeseed crop (Fig. 6), with plant damage and larvae abundance also influenced by these landscape factors. A key determinant of leaf damage and larvae abundance was the direct effect of beetle pressure. Crop heterogeneity influenced larval abundance; however, our structural equation model suggests this is an indirect effect and that larval abundance is primarily driven by beetle pressure. Fisher's C statistic provides an overall estimation of the fit of our piecewise structural equation model (C = 9.14; p = 0.691).

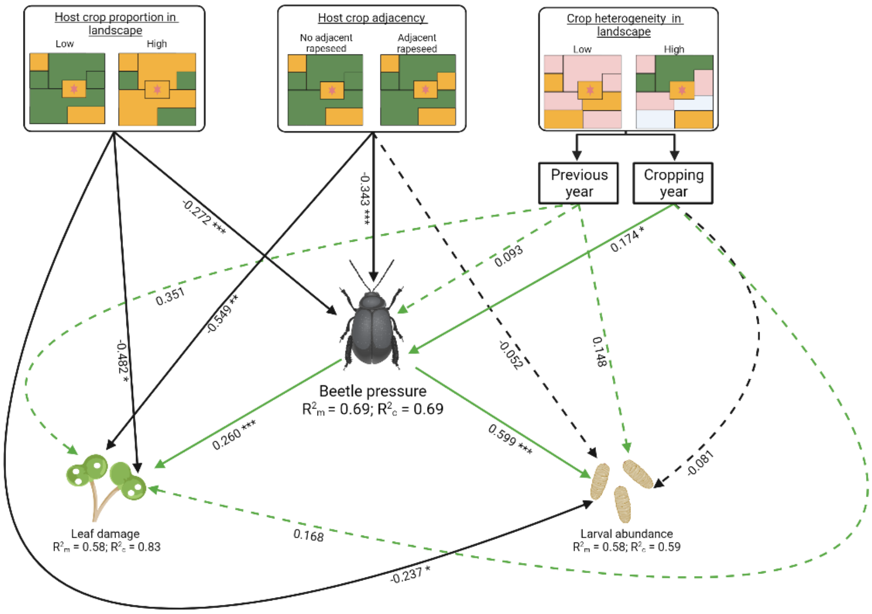

Fig. 6: Piecewise structural equation model. Solid lines denote significant effects. Dashed lines indicate non-significant relationships. Green lines show positive effects and black lines denote negative effects. The numbers along the arrows are standardised path coefficients, and stars mark the significance level (* < 0.05, ** < 0.01, *** < 0.001). In the landscape diagrams: Orange squares denote repassed fields; pale blue, pink, and green squares represent other crop types; red star indicates the focal field. Image was compiled in bioRender.

4. Discussion

In this paper we examined whether the landscape surrounding rapeseed fields influences in-field abundance and crop damage caused by *P. chrysocephala,* a key herbivorous pest of rapeseed. We find that regulation of *P. chrysocephala* populations at the landscape-level is primarily driven through bottom-up processes, with little evidence of top-down suppression. We show that host crop proportion in the landscape, particularly adjacency to another rapeseed crop, is a significant bottom-up regulator of herbivorous pest pressure, crop damage, and larval infestation. These bottom-up processes potentially contribute to herbivorous pest regulation by diluting beetles in the landscape, thereby reducing herbivorous pest pressure and limiting crop damage. We also find that crop heterogeneity in the landscape can influence larval infestation in rapeseed plants, but this is potentially an indirect effect that is mediated by overall beetle pressure. Although we find no direct link between natural enemy populations and beetle pressure (i.e., no direct evidence of top-down regulation of herbivorous pests) we observe bottom-up regulation of natural enemy communities by crop heterogeneity and seminatural habitat at the landscape scale.

4.1 Greater host crop proportion and adjacency to another rapeseed crop reduces herbivorous pest pressure and crop damage

A key finding of our study was that field sites with a higher proportion of rapeseed grown in the same cropping season had lower *P. chrysocephala* pressure, reduced leaf damage, and decreased larval abundance. Lower *P. chrysocephala* pressure suggests a dilution of beetles across the host crops in the surrounding landscape. Similar effects on other herbivorous pests of rapeseed have been observed, including for pollen beetle, stem weevil, brassica pod midge, and other flea beetle species. This includes lower abundance of the asparagus beetle (*Crioceris asparagi*) in fields surrounded by a greater proportion of host crop over a 1 km spatial scale (Zavalnitskaya et al., 2022); Zaller et al., 2008b reported a similar relationship between host crop proportion and pollen beetle insect abundance across several spatial scales. Scheiner and Martin (2020) also observed a reduction in the abundance of leaf-chewing herbivorous pests (including other flea beetle species) in cabbage fields where a greater proportion of host crop was grown in the surrounding landscape, and Josso et al. (2013) described a decrease in the number of cabbage root fly eggs in fields surrounded by a higher proportion of Brassica crops over a 1 km circumference. The observed decrease in the abundance of *P. chrysocephala* (this study), pollen beetle and stem weevil (Zaller et al., 2008b), asparagus beetle (Zavalnitskaya et al., 2022), cabbage root fly (Josso et al., 2013), and general leaf-chewing insects (Scheiner and Martin, 2020) as the proportion of host crop grown in the surrounding landscape increases indicates a dilution effect of foliar-feeding insects across the landscape. This broadly follows the landscape-moderated dilution hypothesis (Tscharntke et al., 2012).

With regards to the relationship between increasing host crop proportion and lower leaf damage: Zaller et al. (2008a) observed a decrease in damage caused by pollen beetles (% of podless peduncles) and pod midge (% of premature pods) as the proportion of rapeseed in the surrounding landscape increased. This is in-line with our observations of reduced *P. chrysocephala* damage and lower larvae abundance at sites surrounded with a greater rapeseed proportion. Our structural equation modelling suggests that the observation of reduced leaf damage and lower larvae abundance is both an indirect bottom-up effect of the landscape and a direct effect of beetle pressure. We also observed an effect of crop heterogeneity on larval abundance, with larval infestation increasing at sites that had a higher crop heterogeneity in the previous season. The structural equation model suggests that larval abundance is primarily mediated by *P. chrysocephala* pressure, with limited direct effect of crop heterogeneity. Crop heterogeneity in the previous year has been reported to influence population densities of similar flea beetle species (*Phyllotreta undulata*) in spring rapeseed fields, with increasing crop heterogeneity over a 2,000 m radii influencing beetle abundance (Boetzl et al., 2023).

These observations indicate that the proportion of host crop habitat in the surrounding landscape is a key driver of herbivorous pest pressure and resulting crop damage in agricultural ecosystems. We also found that presence/absence of a neighbouring rapeseed crop was a key factor determining *P. chrysocephala* pressure and damage, with lower beetle abundance and less damage observed in rapeseed fields that were adjacent to another rapeseed crop. This is in-line with recent research indicating that adjacent habitat influences population dynamics of herbivorous pests, including the herbivorous pests of Brassica crops (Akter et al., 2023).

4.2 Proximity to previous year’s rapeseed crop and influence of natural enemies

We did not detect any influence of previous season host crop proportion on any *P. chrysocephala* parameter measured, indicating that a habitat sink is a more important factor determining *P. chrysocephala* dispersal across a landscape at the examined scales than a habitat source. However, a recent study examining the effects of landscape (previous crop and seminatural habitat) on *P. chrysocephala* at larger spatial scales (10 km) indicated that increased rapeseed proportion in the previous year can influence the probability of larval infestation (Hausmann et al., 2023).

Proximity to previous year's host crop can also affect herbivorous pest pressure (Hausmann et al., 2023; Weisz et al., 1994; Zaller et al., 2008a) and crop damage, including for other flea beetle species (Boetzl et al., 2023) and for *P. chrysocephala* (Hausmann et al., 2023). We did not detect any influence of decreasing proximity to previous year's rapeseed crop. However, the majority of our fields were in relatively close proximity to a previous rapeseed field: 42% were directly adjacent to a previous rapeseed crop and 50% had a previous rapeseed field within 1 km, only one field was more than 1 km away from a previous rapeseed crop. Recent observations of lower *P. chrysocephala* abundance as proximity to previous year's rapeseed crop increased (Hausmann et al., 2023) examined this over a larger spatial scale (10 km).

We did not observe any direct impact of natural enemies on *P. chrysocephala* abundance or any indirect effect on leaf damage and larvae abundance. However, as only a few natural enemies of *P. chrysocephala* have been described (Hoarau et al., 2022) we used proxy measurements for natural enemy groups and may have overestimated natural enemy communities. Nonetheless, the abundance of these arthropod communities was influenced by bottom-up processes at several spatial scales, with influencing landscape factors including crop heterogeneity and the proportion of seminatural habitat. Increased natural enemy abundance at sites surrounded with more seminatural habitat follows previous observations and is likely due to the reliance of these insects on the availability of habitats, refugia, and resources (Martin et al., 2019). Landscapes with greater crop heterogeneity can provide greater resource availability for natural enemies and can thereby support more abundant insect populations, including populations of other herbivorous pests (Boetzl et al., 2023; Redlich et al., 2018). Therefore, the bottom-up processes that regulate natural enemy communities are likely associated with an increased presence and abundance of alternative prey species and increased non-crop habitats that support a greater abundance of non-agricultural insects.

5. Conclusion

Our results confirm emerging research on the importance of year-to-year patterns in host crop amounts in determining the abundance and damage of herbivorous pests in crops. For a key herbivorous pest responsible for major losses in winter rapeseed systems, we show that a high proportion of rapeseed (host crop) in the landscape can decrease herbivorous pest pressure and crop damage, and that adjacency to another rapeseed field can further contribute to diluting pest impacts. Moreover, we show that herbivorous pest pressure is mainly driven by bottom-up processes with no evidence of regulation by natural enemies. Manipulating the agricultural landscape to deliver sustainable herbivorous pest suppression is an approach that has been suggested for similar herbivorous pests. However, implementing these approaches is often difficult as planning at the landscape scale goes beyond the individual farm level and requires integration with multiple stakeholders in order to deliver the benefits (Lundin et al., 2021). Given strong evidence suggesting that *P. chrysocephala* populations, alongside other major herbivorous pests of rapeseed, are regulated by host crop proportions in the agricultural landscape, we recommend the development of collective, landscape-wide crop rotation strategies that enable sustainable management in these major crop systems while minimising the use of synthetic pesticides. Furthermore, given apparent similarities of bottom-up regulation processes for a range of herbivorous pests in rapeseed and other crops, we suggest that exploring the interactive effects between multiple herbivorous pests in the same crop and landscapes would highlight important regulatory landscape-scale processes that could be exploited to achieve synergistic suppression of multiple pest species. Examining the top-down and bottom-up processes that influence herbivorous pest pressure across scales in other understudied organisms will help identify commonalities that can be used to regulate herbivorous pest populations more broadly.

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Ethical statement

No specific permissions applied to this study according to the national legislation.

CRediT authorship

Conceptualisation: DJL, EAM, AMCP. Methodology: DJL, EAM, AMCP. Formal analysis: DJL. Investigation: AMCP, PM, DJL. Data curation: AMCP, DJL. Writing – original draft: DJL. Writing – review and editing: EAM. Visualisation: DJL. Supervision: DJL, EAM. Funding acquisition: DJL. EAM.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data and code are available open access via the University of Liverpool Research Data Catalogue (Leybourne et al., 2023): https://datacat.liverpool.ac.uk/2511/ To protect privacy of the participating farmers we are unable to publicly share geodata associated with the project. This information can be requested by contacting the corresponding author.

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