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# Flea beetles in spring oilseed rape differ in phenology and habitat choices for reproduction and overwintering—Implications for pest management

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## Abstract

1. Spring oilseed rape is severely affected by early season herbivory of various flea beetle species. Flea beetle pest management strategies with less reliance on conventional chemical insecticides are direly needed. However, the current knowledge of flea beetle ecologies and life cycles is insufficient to design and inform such strategies effectively.
2. Using a combination of pitfall and emergence traps, we followed the life cycles of flea beetles in 13 spring oilseed rape fields in south central Sweden, measuring densities in three sampling seasons: spring activity at crop seedling stage, summer emergence of the new generation, and emergence of overwintered adults in the following spring in the adjacent grassy field margins.
3. We found a strong positive relationship between densities of emerging *Phyllotreta atra*, *P. striolata* and *P. undulata* in summer and their densities earlier in spring. Flea beetle assemblage composition differed across the seasons, driven by changes in the relative abundances of different species. While assemblages emerging in summer were filtered for species reproducing in spring oilseed rape, assemblages emerging from the grassy field margins in the following spring were again more heterogeneous.
4. Spring activity peaks and summer emergence peaks differed among species, with *P. vittula* having an earlier activity peak and emerging earlier than most other species.
5. This knowledge of spatiotemporal habitat use can contribute to a more effective flea beetle management in spring oilseed rape. Especially summer emergence in the fields became apparent as a so far unexplored point in time to control flea beetle pests.

KEYWORDS
*Brassica napus*, flea beetle, integrated pest management (IPM), neonicotinoid ban, pest regulation, Phyllotreta

# INTRODUCTION

Spring oilseed rape (*Brassica napus* L.) is an important cash and break crop in the cereal-dominated cropping systems of the boreal and hemi-boreal regions where winter oilseed rape cannot be grown (Cornelsen et al., 2024; Lundin, 2021). Protection of spring oilseed rape against a number of specialised insect herbivores depends largely on the use of insecticides (Ekbom, 2010; Li et al., 2024). Especially early-season attacks on the emerging oilseed rape seedlings by flea beetles can lead to severe yield losses later in the season (Lamb, 1984; Lundin, 2020). Systemic neonicotinoid seed coatings were widely used in the European Union to protect oilseed rape seedlings against flea beetle attacks until their use was restricted in 2013 (Kathage et al., 2018). Less effective systemic and non-systemic insecticides have replaced them since (Kathage et al., 2018; Lundin, 2021). Thus, alternative methods for pest regulation are needed, also in the light of policy development towards pesticide use reduction, particularly in the European Union (Lee et al., 2019). Pest management in spring oilseed rape would benefit from an improved understanding of the ecology of its flea beetle pests, to inform pest regulation with less dependency on chemical insecticides.

The basics of pest flea beetle life cycles in spring oilseed rape are well understood (Dosdall & Mason, 2010; Ekbom, 2010). Ekbom (2010) lists five *Phyllotreta* species as commonly occurring in spring oilseed rape fields in Europe, four of which as well as two *Chaetocnema* species are common in the crop in Sweden (Boetzl et al., 2023). With a few exceptions detailed below, their life cycles are similar. The flea beetles colonise spring oilseed rape fields early in the season when the cotyledons emerge (Ekbom, 2010; Li et al., 2024). The beetles feed on the young oilseed rape seedlings (Figure 1a), reproduce in the fields and lay their eggs at the base of the stems (Ekbom, 2010; Li et al., 2024). *Phyllotreta vittula* and *Chaetocnema* spp. differ from the other species, as while they were observed feeding on oilseed rape, they are believed not to reproduce in the crop (Boetzl et al., 2023; Ekbom, 2010). After hatching, the larvae of *P. atra*, *P. striolata* and *P. undulata* move into the soil and feed on the roots until they pupate, the adult beetles emerging later in summer (Ekbom, 2010). The beetles subsequently disperse and seek suitable habitats for overwintering (Boetzl et al., 2024; Ekbom, 2010). In the following year, when the soil has warmed up, the overwintering flea beetles emerge and immigrate to newly sown spring oilseed rape fields (Kocourek et al., 2002; Lamb, 1983). Despite their economic importance, gaps remain in the understanding of flea beetle life cycles, for example whether and how species differ in the timing of certain life-history stages, where flea beetles overwinter and how this varies among species.

Overwintering habitat preferences have been examined for flea beetles occurring in spring canola/oilseed rape in North America, but such studies are missing for Europe. *Phyllotreta cruciferae* and *P. striolata* overwinter in leaf litter and the top soil in various uncultivated habitats such as harvested oilseed rape stubble fields, grassy shelterbelts, hedgerows and tree groves in Canada, with *P. cruciferae* overwintering in highest densities in hedgerows and *P. striolata* in tree groves (Burgess, 1977; Burgess, 1981). *Phyllotreta cruciferae* preferred sheltered habitats (tree groves, shrubs) as overwintering sites over open grasslands in Canada (Ulmer & Dosdall, 2006). The cabbage stem flea beetle, a pest on winter oilseed rape, aestivates in woodland edges in summer (Pigot et al., 2024). In Sweden, we found that the proximity to host crop fields in the previous year predicts flea beetle densities across species, as well as the resulting crop damage in spring oilseed rape in the following year (Boetzl et al., 2023). This indicates that a majority of the pest flea beetles overwinter close to the host crop field, with grassy field margins adjacent to the spring oilseed rape field being a potential yet unexplored overwintering habitat in these landscapes.

Aiming to understand better the ecology of flea beetles in spring oilseed rape, we followed flea beetle assemblages in 13 spring oilseed rape fields in south central Sweden for one complete life cycle. We recorded assemblages feeding on oilseed rape seedlings in spring,

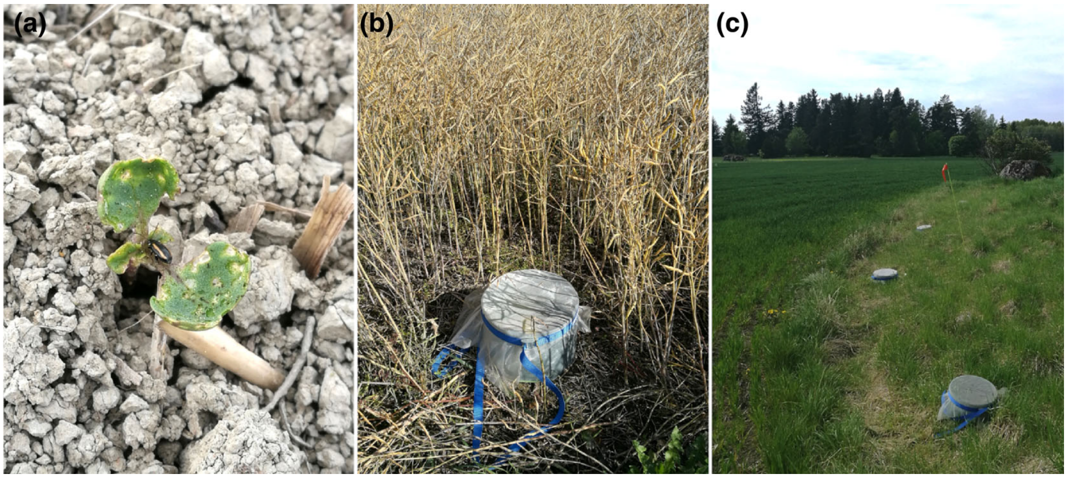

**FIGURE 1** *Phyllotreta undulata* feeding on spring oilseed rape seedling in spring (a), emergence trap collecting emerging flea beetle assemblages in a spring oilseed rape field in summer (b) and emergence traps collecting flea beetle assemblages emerging from overwintering in the adjacent grassy field margin in the following spring (c). Pictures: Ola Lundin.

collected offspring assemblages emerging from the crop fields in summer and collected assemblages emerging from overwintering in grassy margins adjacent to the crop fields the following spring. With this information, we identified similarities and differences among economically relevant flea beetle species in their spatio-temporal patterns of habitat use to better inform pest regulation strategies. We first compared the relative proportion and assemblage composition of flea beetle species at the three time points: spring activity in oilseed rape fields, summer emergence from oilseed rape fields and subsequent spring emergence from field edges adjacent to the crop fields. We further assessed the correlation of flea beetle abundances between these time points: spring to summer, and summer to subsequent spring. We interpret positive correlations between time steps as the species successfully progressing to the next stage in the life cycle in the examined habitat, whereas an absence of correlation could indicate limited reproduction success or a change of habitat. Finally, to explore differences in phenology, we compared the abundance-weighted species-specific peaks in activity or emergence at each of the three time points in the flea beetle life cycle.

## MATERIALS AND METHODS

### Study design and data collection

Flea beetle assemblages were sampled from spring 2018 to spring 2019 in 13 conventionally managed spring oilseed rape fields and the adjacent grassy margins. The 13 fields were distributed in Stockholm, Uppsala, and Västmanland counties in south-central Sweden, a region with high cover of arable land and many embedded forest fragments (Supplementary Figure S1). The cover of arable land ranged from 34.8% to 90.5% (mean ± SE: 65.2 ± 5.7%), forest cover from 1.7% to 48.8% (mean ± SE: 20.6 ± 4.4%) and the cover of pastures from 0.8% to 16.6% (mean ± SE: 6.8 ± 1.3%; all within 1000 m radius; for effects of the surrounding landscape on flea beetles in spring oilseed rape, see Boetzl et al. (2023)). The minimum distance between sampled plots was 3122 m and field sizes ranged between 2.6 and 55.2 ha (mean ± SE: 23.1 ± 4.5 ha; Supplementary Table S1). All fields were sown with spring oilseed rape without insecticide seed treatments between 27 April and 22 May 2018 (Supplementary Table S1). Several commonly grown cultivars, both conventional and Clearfield®-type, were included among the fields studied.

In each field, we established a sampling plot located immediately adjacent to one of the field edges. The sampling plots were 50 m long and 24 m wide (area: 1200 $m^2$), except in one site where the plot was 18 m wide due to the spraying machinery available at this farm (area: 900 $m^2$). No foliar insecticides against flea beetles were used in the sampling plots during the experiment. The sampling plots otherwise received the same management as the rest of the field, including herbicide applications.

In spring of the first year, flea beetles were sampled using wet pitfall traps (height: 11 cm, diameter: 11.5 cm) placed in each corner of the sampling plots at a distance of 1 m from the plot edges, resulting in four pitfall traps per plot with a minimum distance of 10 m between pitfall traps. Pitfall traps were installed and activated within 4.7 ± 0.7 days after crop sowing and before any plants had emerged (mean ± SE; range: 1 to 10 days). Pitfall traps were active between 10 May and 06 July 2018, with slight shifts among sites due to differences in sowing dates and crop development rates. Traps were emptied every 2 to 4 days until the crop had two fully developed true leaves, resulting in 18 to 46 days of pitfall trapping as oilseed rape growth rate varied across sites. The relatively slow crop establishment in some sites was due to a drought that delayed germination and emergence in sites lacking soil moisture at sowing. Accounting for occasional trap losses, the total accumulated pitfall trap days per sampling plot ranged from 72 to 181 days with all four traps combined (mean ± SE: 105.6 ± 8.9 trapping days; 1 trapping day = 1 day of one active pitfall trap).

We measured flea beetle emergence in the plots in summer with emergence traps (Figure 1b). In each plot, we placed four emergence traps approximately equidistant along a transect running in the centre of the plot, parallel to the field edge. Each emergence trap consisted of a circular metal barrier (diameter 35 cm; height: 30 cm; area: 0.096 $m^2$) dug into the ground at least 10 cm deep and covered with a fine mesh (mesh size: <0.5 mm). In each emergence trap, we mounted three double-sided yellow sticky traps (10 × 5 cm) horizontally approximately 2 cm above the ground on toothpicks, to catch emerging flea beetles. The emergence traps were active between 10 July and 30 August 2018, which approximately covered the summer emergence interval for flea beetles in spring oilseed rape in high latitudes (Boetzl et al., 2024).

In the following spring, we set up the same emergence traps in the adjacent grassy field margins to record flea beetles emerging from overwintering (Figure 1c), We chose grassy margins based on literature information on overwintering habitats of the focal species (Burgess, 1981). Four emergence traps were placed about 1 m from the field edge inside the grassy margins, with a distance of 5 m between the emergence traps. In spring, emergence traps were active between 01 April and 07 June 2019, when overwintering individuals become active and disperse into crop fields (Kocourek et al., 2002). The limited replication of the study and the plethora of possible overwintering habitats allowed us only to have emergence traps in grassy margins, but this was the most common adjacent non-crop habitat type.

In both intervals, the set-up and collection dates shifted slightly within a range of 4 days across sites. Visualisation of the emergence data confirmed that both emergence periods were adequately covered given that, in most cases, no individuals were collected at the start and the end of the sampling (Supplementary Figure S2). The sticky traps in each emergence trap were exchanged weekly. In the summer interval, one sticky trap in one emergence trap was lost due to a handling mistake. After collection, all sticky traps were frozen at −20°C until flea beetles were identified. All flea beetles in the pitfall trap samples and on the sticky traps were identified to species or genus level (Table 1).

**TABLE 1** Total and per day catches (total number divided by the total number of days traps were active; both rounded to two decimals) as well as proportions (of all caught individuals, rounded to two digits) of flea beetles in three sampling intervals: spring (activity measured with pitfall traps), summer (emergence measured in emergence traps), and spring of the following year (emergence measured in emergence traps) across 13 spring oilseed rape fields in south-central Sweden 2018–2019. Selected taxa with comparably high abundance are highlighted in bold.

| | Spring activity | | | Summer emergence | | | Spring emergence | | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Genus or species | Total | Per day | Proportion [%] | Total | Per day | Proportion [%] | Total | Per day | Proportion [%] | Abundance | Proportion [%] |
| *Aphthona euphorbiae* | 111 | 0.08 | 2.70 | 75 | 0.01 | 1.05 | 16 | < 0.01 | 1.03 | 202 | 1.57 |
| *Bathophila rubi* | | | | 63 | 0.01 | 0.88 | 3 | < 0.01 | 0.19 | 66 | 0.51 |
| *Bathophila* sp. | 1 | < 0.01 | 0.02 | | | | | | | 1 | 0.01 |
| ***Chaetocnema concinna*** | **357** | **0.26** | **8.96** | **77** | **0.01** | **1.07** | **30** | **< 0.01** | **1.93** | **464** | **3.61** |
| ***Chaetocnema mannerheimi*** | **396** | **0.29** | **9.64** | **12** | **< 0.01** | **0.17** | **37** | **< 0.01** | **2.38** | **445** | **3.47** |
| *Haltica* sp. | | | | 2 | < 0.01 | 0.03 | 1 | < 0.01 | 0.06 | 3 | 0.02 |
| *Longitarsus* sp. | 57 | 0.04 | 1.39 | 16 | < 0.01 | 0.22 | 22 | < 0.01 | 1.42 | 95 | 0.74 |
| *Lythraria salicariae* | | | | 46 | 0.01 | 0.64 | 10 | < 0.01 | 0.64 | 56 | 0.44 |
| *Mantura rustica* | 4 | < 0.01 | 0.10 | 1 | < 0.01 | 0.01 | 7 | < 0.01 | 0.45 | 12 | 0.09 |
| ***Phyllotreta atra*** | **870** | **0.63** | **21.18** | **1237** | **0.14** | **17.24** | **101** | **0.01** | **6.50** | **2208** | **17.20** |
| *Phyllotreta nigripes* | 10 | 0.01 | 0.24 | 140 | 0.02 | 1.95 | 47 | < 0.01 | 3.03 | 197 | 1.53 |
| ***Phyllotreta striolata*** | **513** | **0.37** | **12.49** | **722** | **0.08** | **10.06** | **31** | **< 0.01** | **2.00** | **1266** | **9.86** |
| ***Phyllotreta undulata*** | **1386** | **1.01** | **33.74** | **3009** | **0.35** | **41.93** | **270** | **0.03** | **17.39** | **4665** | **36.34** |
| ***Phyllotreta vittula*** | **402** | **0.29** | **9.79** | **1777** | **0.21** | **24.76** | **976** | **0.09** | **62.85** | **3155** | **24.58** |
| *Psylliodes chrysocephala* | | | | | | | 2 | < 0.01 | 0.13 | 2 | 0.02 |
| *Psylliodes* sp. | 1 | < 0.01 | 0.02 | | | | | | | 1 | 0.01 |
| **Total** | 4108 | 2.99 | 100 | 7177 | 0.84 | 100 | 1553 | 0.15 | 100 | 12,838 | 100 |

## Statistical analyses

All statistical analyses were performed in R 4.3.0 for Windows (R Development Core Team, 2024). For most of the analyses, we used the six species with the highest overall catches *Phyllotreta atra*, *P. undulata*, *P. striolata*, *P. vittula*, *Chaetocnema concinna* and *C. mannerheimi* (Table 1). These species are all known crop pests. For all analyses, we pooled all samples from the same collection date, for most analyses also within the same sampling season.

In a first step, we compared collected flea beetle assemblages in the three sampling seasons, that is spring, summer and the following spring. For this, we transformed species abundances in each season and field to relative abundances (i.e., proportional shares of the assemblages) to focus on assemblage changes rather than changes in total abundances and to minimise any potential effects of the different trap types used. We compared the share of the assemblage across the three sampling seasons for the six selected species using linear mixed effects models (LMM, command 'lmer' from the package 'lme4', version 1.1-33 (Bates et al., 2015)) with 'sampling season' (factor, three levels) as fixed effect and 'field ID' as random intercept and Gaussian residual distributions. We compared flea beetle assemblage composition across the three sampling seasons using non-metric multidimensional scaling (NMDS, 'metaMDS', 999 permutations, Bray–Curtis distances) using the species matrix with relative abundances. We tested for statistically significant differences between the three sampling seasons (factor, three levels) using a permutational multivariate analysis of variance (PERMANOVA; 'adonis2' from the 'vegan' package, version: 2.6-4 (Oksanen et al., 2019); 9999 permutations, Bray–Curtis distances) including field identity as strata object due to repeated sampling in the same fields. Separate NMDS and PERMANOVA were performed for all recorded flea beetles and for the six selected species. In addition, we calculated Pearson correlations between the activity densities of flea beetles active in spring and activity densities of flea beetles emerging in the same fields in summer (an indication for reproduction in the field) as well as between the activity densities of flea beetles emerging in summer and the activity densities of flea beetles emerging in the following spring in the adjacent grassy margins (an indication of overwintering). Activity densities were calculated as individuals per day and trap.

In a second step, we compared the activity windows of the selected flea beetle species across the three sampling seasons. We calculated abundance weighted average activity or emergence dates, as day of the year (DOY), for each of the six focal species in each field and sampling season. Within each season, we compared the abundance weighted average DOY of each species using a LMM with the same specifications as stated above but including 'species' (factor, six levels) instead of sampling season as fixed effect.

All LMMs were carefully checked using the packages 'performance' (version 0.10.4 (Lüdecke et al., 2021)) and 'DHARMa' (version 0.4.6 (Hartig, 2022)) and fulfilled all assumptions. We obtained $p$-

**TABLE 2** Densities (per square meter) of emerging flea beetles of six selected species in the 13 spring oilseed rape (SOSR) fields in south-central Sweden in the summer of 2018 and in adjacent grassy field margins in the following spring in 2019. Average across all sites and the range with minimum and maximum (values rounded to integers).

| | Summer emergence (SOSR field) | | Spring emergence (field margins) | |
|---|---|---|---|---|
| Genus or species | Individuals per m$^2$ | Range [min; max] | Individuals per m$^2$ | Range [min; max] |
| *Chaetocnema concinna* | 16 | [0; 102] | 6 | [0; 18] |
| *Chaetocnema mannerheimi* | 3 | [0; 8] | 7 | [0; 26] |
| *Phyllotreta atra* | 248 | [8; 1266] | 20 | [0; 86] |
| *Phyllotreta striolata* | 145 | [31; 617] | 6 | [0; 39] |
| *Phyllotreta undulata* | 603 | [125; 2393] | 54 | [3; 234] |
| *Phyllotreta vittula* | 356 | [16; 1732] | 195 | [3; 1156] |

values via type II Wald F-tests and degrees of freedom via the Kenward–Roger approximation ('Anova' command in package 'car', version 3.1–2 (Fox & Weisberg, 2019)). Pairwise contrasts were obtained using the 'emmeans' command (package 'emmeans', version 1.8.6 (Lenth, 2022)).

# RESULTS

In total, we collected 12,838 flea beetles of 16 taxa across all sites and methods (Table 1). The six species selected for the majority of further analyses accounted for a combined 95.1% of all flea beetles caught. *Phyllotreta undulata* was most common with 4665 individuals (36.3%), followed by *P. vittula* with 3155 individuals (24.6%), *P. atra* with 2208 individuals (17.2%), *P. striolata* with 1266 individuals (9.9%), *Chaetocnema concinna* with 464 individuals (3.6%) and *Chaetocnema mannerheimi* with 445 individuals (3.5%; Table 1). All six selected species apart from the *Chaetocnema* species were found emerging from spring oilseed rape fields in summer in considerably high densities of up to 603 individuals per square metre (*P. undulata*; Table 2). Densities emerging in the adjacent grassy field margins in the following spring were considerably lower, generally less than 10% of those emerging in summer, except for *P. vittula* and the *Chaetocnema* species (Table 2).

## Assemblage composition

Comparing the assemblages recorded at the three sampling seasons, we found that only *P. atra* had a stable share in assemblages across seasons (Figure 2a; Tables 1 and 3). The share of *P. striolata* individuals in spring and emerging in summer were similar, but dropped in the assemblage emerging in the following spring in the grassy margins (Figure 2a; Tables 1 and 3). *Phyllotreta vittula* showed an opposite pattern: it had a lower share in the assemblages active in spring, became more abundant in summer, and had the largest share in the following spring (Figure 2a; Tables 1 and 3). *Phyllotreta undulata* had similar shares in both spring assemblages and a higher share in the assemblages emerging in summer (Figure 2a; Tables 1 and 3). Both *Chaetocnema* species had the highest shares in assemblages active in spring, and were subsequently almost absent in assemblages emerging in summer and the following spring (Figure 2a; Tables 1 and 3).

These shifts in assemblage composition were also visible in the ordinations. While assemblages of flea beetles active in spring differed considerably across sites, we observed an assemblage shift towards more homogenous assemblages of emerging flea beetles with a lower dispersion across sites in summer (Figure 2b). Spring emergence in the field margins in the following year again produced more heterogeneous assemblages across sites considering all flea beetle taxa (PERMANOVA: $F_{2,36} = 7.84$, $r^2 = 0.30$, $p < 0.001$; Figure 2b). This pattern remained similar when considering only the six selected species (PERMANOVA: $F_{2,36} = 5.17$, $r^2 = 0.22$, $p < 0.001$; Figure 2c). In both ordinations, the homogenous assemblages emerging after reproduction in summer clustered closer with the assemblages emerging after overwintering in the following spring.

The activity densities of individuals active in spring and individuals emerging in summer were strongly positively correlated in *P. atra* (Pearson: $r = 0.97$, $p < 0.001$), *P. striolata* (Pearson: $r = 0.96$, $p < 0.001$), *P. undulata* (Pearson: $r = 0.98$, $p < 0.001$) and to a lesser degree *C. concinna* (Pearson: $r = 0.56$, $p = 0.044$), but not in the remaining species (Pearson: $r \leq 0.45$, $p \geq 0.118$; Figure 2d). No significant correlations were found for any of the species between the activity densities of individuals emerging in summer and individuals emerging in the following spring (Pearson: $-0.22 \leq r \leq 0.20$, $p \geq 0.520$; Figure 2e).

## Activity windows

The six species differed in activity peaks in the three time periods. In spring, the peak activites of *P. vittula*, *C. concinna* and *C. mannerheimi* were 6 to 14 days earlier than the peak activities of *P. atra*, *P. striolata* and *P. undulata*, and among early species, the peak activity of *C. mannerheimi* was 7 days earlier compared to *C. concinna* (Figure 3; Table 3). In summer, *P. vittula* had its peak emergence 12 and 13 days before the peak of *P. atra* and *C. concinna* with *P. undulata*, *P. striolata* and *C. mannerheimi* being intermediate between them (Figure 3;

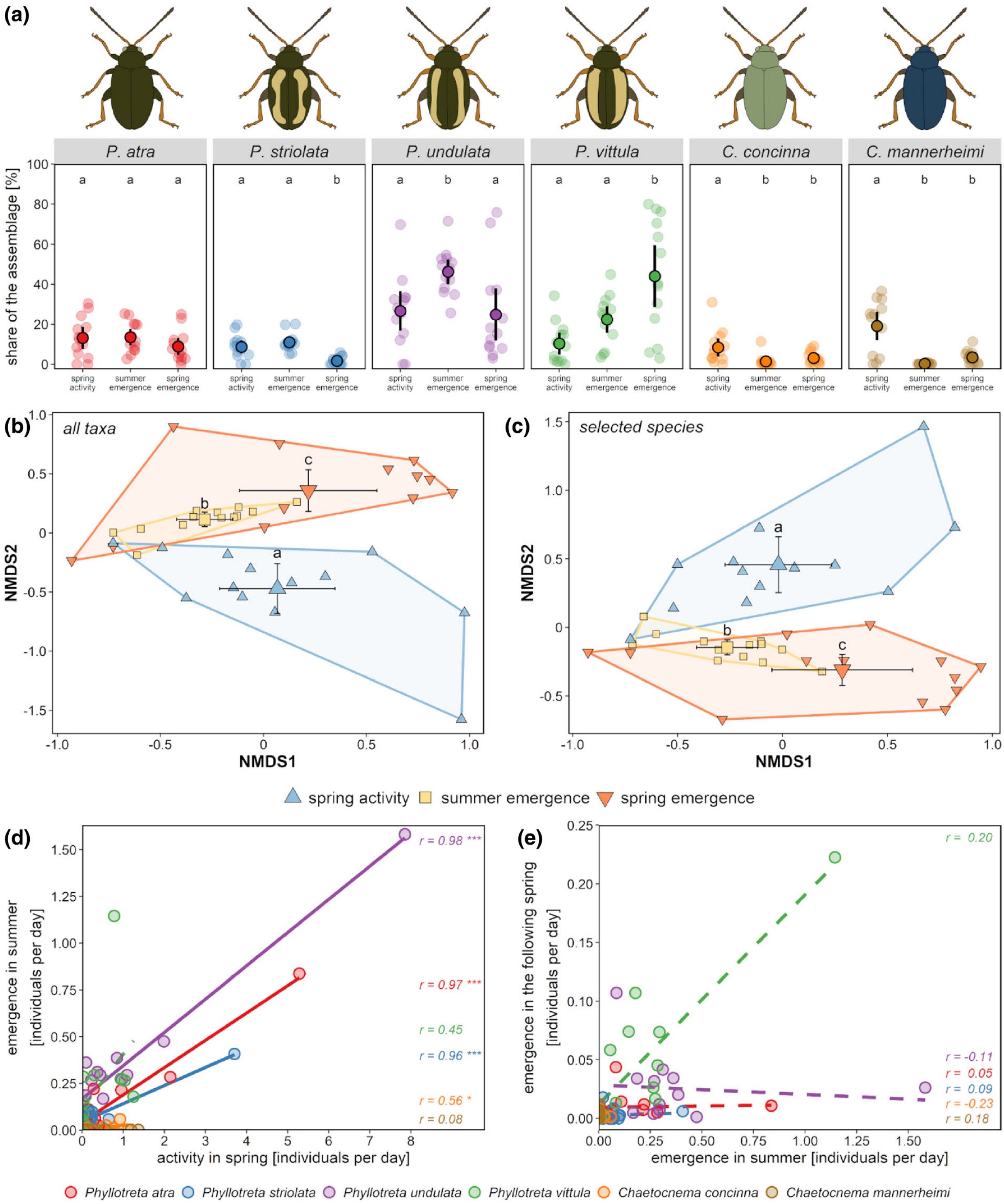

**FIGURE 2** (a) Relative shares of the assemblages of the six most abundant flea beetle species in the three sampling seasons (spring activity, summer emergence, and spring mergence in the following year; mean ± 95% confidence interval) in 13 spring oilseed rape fields in south-central Sweden from spring 2018 to spring 2019. Different letters indicate statistically significant differences ($p < 0.05$). (b, c) NMDS ordinations for the whole flea beetle assemblages (b) and the six selected species (c) in the three sampling seasons based on proportional abundances. Larger symbols represent centroids with 95% confidence intervals, different letters above the centroid indicate statistically significant differences (with $p < 0.05$) between the clusters based on pairwise PERMANOVA tests. For statistics, see text. (d, e) Relation between the densities of flea beetles emerging within spring oilseed rape fields in summer and the densities of flea beetles active in the same fields in spring (d) and between the densities of flea beetles emerging in the field margins in the spring of the following year and densities of flea beetles emerging within spring oilseed rape fields in summer (e) for the six selected species. Solid lines indicate significant correlations ($p < 0.05$), dashed lines indicate non-significant correlations ($p > 0.05$). For a species by species version of (d) and (e), see Figure S4. The r-value stated is the Pearson correlation coefficient. For statistics, see text. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

**TABLE 3** Results for models assessing the effects of sampling season (i.e., spring activity, summer emergence and spring mergence in the following year) on the assemblage shares of six selected flea beetle species and differences between the activity or emergence peaks between them. These results are visualised in Figures 2 and 3. For models specifications, see text. Df, degree of freedom (numerator, denominator); *F*, *F*-value; *p*, *p*-value; $R^2_m$, marginal $R^2$.

| | Fixed effect | Df | *F* | *p* | $R^2_m$ |
|---|---|---|---|---|---|
| Assemblage composition | | | | | |
| *Chaetocnema concinna* | Sampling season | 2, 24 | 8.19 | **0.002**** | 0.24 |
| *Chaetocnema mannerheimi* | Sampling season | 2, 24 | 22.80 | **< 0.001***** | 0.53 |
| *Phyllotreta atra* | Sampling season | 2, 24 | 2.54 | 0.099 (*) | 0.06 |
| *Phyllotreta striolata* | Sampling season | 2, 24 | 15.44 | **< 0.001***** | 0.45 |
| *Phyllotreta undulata* | Sampling season | 2, 24 | 6.75 | **0.005**** | 0.22 |
| *Phyllotreta vittula* | Sampling season | 2, 24 | 19.03 | **< 0.001***** | 0.36 |
| Activity windows | | | | | |
| Spring activity | Taxon | 5, 52 | 17.26 | **< 0.001***** | 0.18 |
| Summer emergence | Taxon | 5, 52 | 10.70 | **< 0.001***** | 0.27 |
| Spring emergence | Taxon | 5, 50 | 0.97 | 0.445 | 0.07 |

*Note*: Statistically significant *p*-values ($p < 0.05$) are highlighted in bold.
(*) indicates $p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table 3). In the following spring, we found no significant differences between emergence peaks among species (Figure 3; Table 3).

# DISCUSSION

Following the life cycles of pest flea beetles of spring oilseed rape in 13 fields in south central Sweden across 1 year, we found that most, but not all, species present in and feeding on spring oilseed rape seedlings also reproduce in spring oilseed rape fields. A subset of species overwinter in large numbers in the adjacent field margins, leading to considerable shifts in flea beetle assemblages over time. In addition, flea beetles show inter-species variation in their peak spring activity and summer emergence, but not in spring emergence.

## Assemblage changes and implications for pest regulation

Flea beetle assemblages changed noticeably across the year. While flea beetle assemblages in spring were dominated by *P. atra*, *P. undulata* and *C. mannerheimi*, this dominance pattern changed with *P. undulata* becoming more dominant while *C. mannerheimi*, and to a lesser degree also *C. concinna*, became less common in the assemblages emerging in summer. During emergence in the following spring, *P. vittula* became more dominant and *P. striolata* and *P. undulata* less dominant in the assemblages. As these observations are based on a single year, they should be confirmed in future assessments. It is further possible that the assemblage shifts between the seasons partly depended on the use of different trap types required for monitoring different life cycle stages: Pitfall traps for spring activity and emergence traps for summer and spring emergence. However, we used relative instead of absolute abundances to minimise such effects, and we are not aware of any biological differences among species rendering them differently susceptible to the two trap types. This would suggest that the trap type had a negligible effect on assemblage composition estimates.

While we observed species of the genus *Chaetocnema* occasionally feeding on spring oilseed rape plants in the field, they are generally not regarded as *Brassica* pests and only few species are known to feed on Brassicacae (Konstantinov et al., 2011). Several species of the genus *Chaetocnema* reproduce and are commonly found in spring cereals such as barley, wheat and oats (Blunck, 1932). *Chaetocnema mannerheimi* is a pest on spring barley (Rosen, 1984), while *C. concinna* feeds on various Polygonaeceae, including *Rumex* sp. which are common weeds in the region, and is known as an occasional pest on beets and buckwheat (Konstantinov et al., 2011). Based on our results, it seems likely that both *Chaetocnema* species feed as adults in the spring oilseed rape fields, mainly on non-crop but also crop plants. The species then mostly disperse in late spring and reproduce and overwinter elsewhere (*C. mannerheimi*) or partly stay and reproduce on weeds in the spring oilseed rape field (*C. concinna*).

Flea beetle assemblages emerging in summer clearly represented a selected, homogenous subset of those active in spring. These assemblages emerging in summer predominantly contained species that are closely associated, feed on and reproduce in spring oilseed rape fields, with the capacity to reproduce in spring oilseed rape fields likely acting as the strongest filter. This reveals a possible opportunity for the regulation of flea beetles in spring oilseed rape: as flea beetle pests have only one generation per year, managing the emerging adults in summer in spring oilseed rape fields could reduce flea beetle infestations in spring oilseed rape fields in the following year. This is especially promising considering that the flea beetle population size in autumn is positively related to crop damage in the subsequent season (Boetzl et al., 2024). One possibility would to be deploy odor-baited

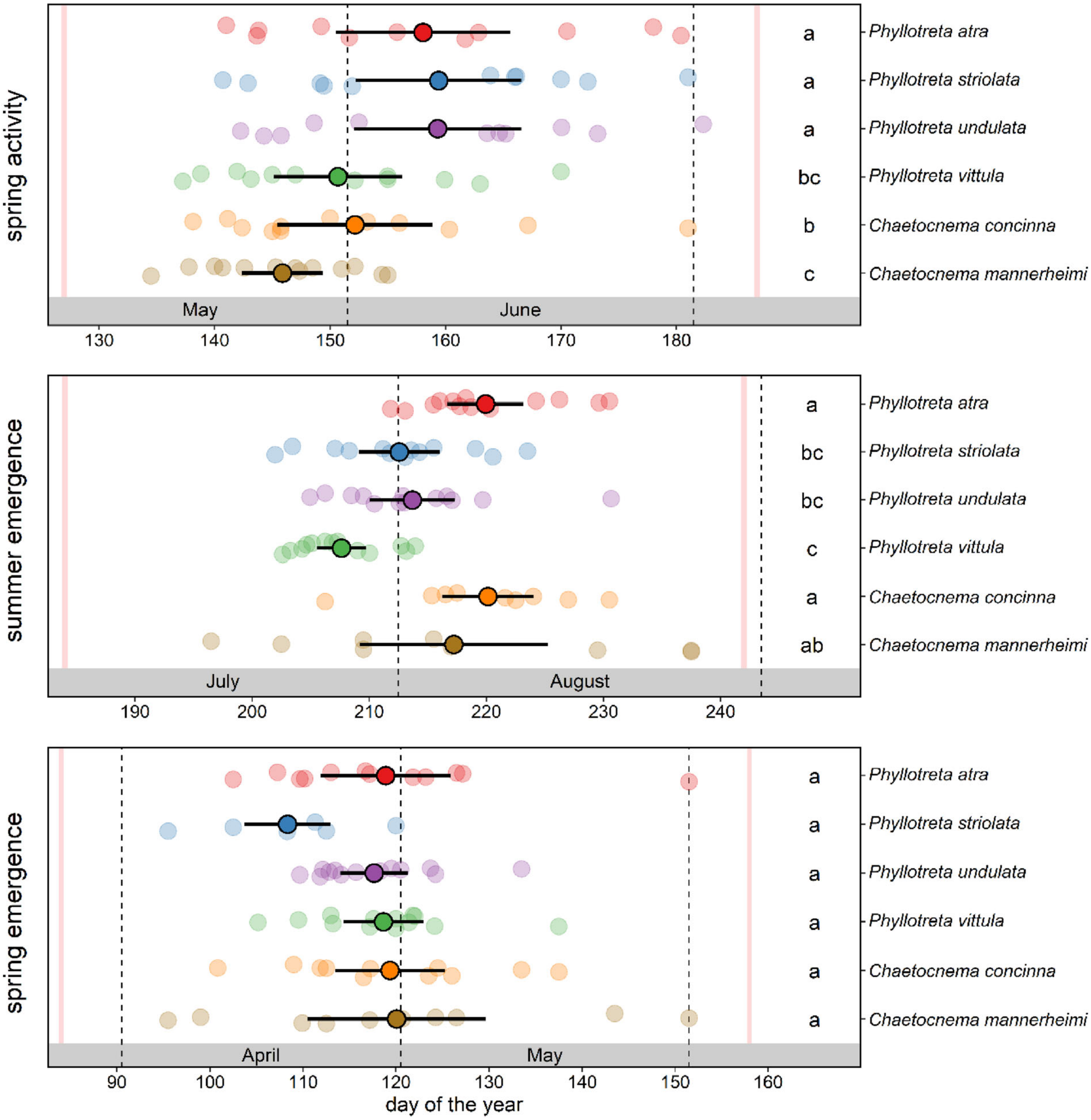

**FIGURE 3** Abundance weighted average peak of spring activity (top), summer emergence (middle) and spring emergence in the following year (bottom) of the six most abundant flea beetle species. Black horizontal lines indicate the 95% confidence interval of the mean. Thin, vertical dashed lines represent the turn of months, red vertical solid lines indicate the start and endpoints of the sampling in all three seasons. Different letters on the right indicate statistically significant differences (with $p < 0.05$).

traps at the time of summer flea beetle emergence for pest management (Beran et al., 2011; Pivnick et al., 1992), although host plant volatiles or pheromones might be less attractive to flea beetles in this stage of their life cycle. A drawback of management aimed at regulating flea beetles at the time of summer emergence is, however, the spatial and temporal mismatch to any reduction in pest damage that will only occur in the next season and not necessarily in a crop field managed by the same farmer who spent resources on treating against the pests. Such pest management strategies thus require collective and landscape-scale approaches (Brewer & Goodell, 2012).

All species were found overwintering and emerging from the grassy field margins, but their use of field margins for overwintering differed across species. In addition, the assemblages emerging at the margins in spring were more heterogeneous than the assemblages emerging in summer within spring oilseed rape fields. Assemblages emerging from the field margins were, however, also different from the assemblages active in the fields during the previous spring, indicating that a considerable share of the assemblages colonises the spring oilseed rape fields from habitats other than grassy field margins.

The assemblages of flea beetles emerging in the following spring in the grassy field margins were dominated by *P. vittula*. At first glance, this was unsurprising as this species was thought to reproduce only in cereals (Blunck, 1932; Ekbom, 2010), which is the most common crop type in the study region. However, we observed *P. vittula* in considerable densities during crop establishment in spring and emerging from spring oilseed rape fields in summer (Table 2) indicating that the species does, in fact, also reproduce in spring oilseed rape fields. It, however, remains unclear whether reproduction happens on oilseed rape, weeds or cereal volunteers. In contrast to the other *Phyllotreta* species for which spring activity and summer emergence densities were strongly positively correlated, we found no such relation for *P. vittula*, suggesting a less obligate relationship to reproduction in the spring oilseed rape field for *P. vittula*.

*P. striolata* and *P. undulata* decreased in proportional share of the assemblage, and all species were less abundant in the assemblages emerging in spring compared to those emerging in summer (Table 2). This indicates that a considerable share of individuals and especially the species *P. striolata* and *P. undulata* move into other, more suitable habitats in the surrounding landscape for overwintering. In a correlative landscape-scale study we found positive effects of forest cover in the landscape surrounding spring oilseed rape fields only for *P. undulata* (Boetzl et al., 2023), indicating that this species benefitted from and likely overwinters in forests. Based on studies from Canada, *P. striolata* prefers woody, sheltered habitats for overwintering (Burgess, 1977; Burgess, 1981). The abundance of *P. striolata* was also negatively related to edge-density in the landscapes surrounding spring oilseed rape fields, suggesting that the species does not benefit from edge structures (Boetzl et al., 2023). Another possibility is that these species and a considerable share of the individuals do not move to the field margins, but instead overwinter directly in the oilseed rape stubble fields, as found in *P. striolata* and other flea beetles in Canada (Burgess, 1977; Burgess, 1981). Crop fields are used by many mostly ubiquitous and generalist arthropod species for reproduction and overwintering (Boetzl et al., 2022; Hoffmann et al., 2021). In addition, differences in overwintering mortality among flea beetle species could explain the observed changes in densities and proportional shares, at least in part (Turnock et al., 1987). Based on our results, grassy field margins adjacent to spring oilseed rape fields are likely not a suitable target for direct flea beetle pest management through disruption of their life cycles as measures would only affect a smaller share of the individuals present in a landscape and colonising spring oilseed rape fields in spring. They could, however, indirectly promote pest regulation through supporting natural enemies of flea beetles (Boetzl et al., 2023).

## Adapting pest regulation to flea beetle phenology

The community-weighted peaks of spring activity in spring oilseed rape fields were similar in *P. atra*, *P. striolata* and *P. undulata*, but earlier in *P. vittula* and the two *Chaetocnema* species. As all six species were recorded in at least some of the fields within the first days of trapping, this earlier activity peak was not caused by an earlier arrival of these species to the fields. In especially *P. vittula*, and to a lesser degree both *Chaetocnema* species, fewer individuals were caught within the last 2 weeks of pitfall trapping which could explain the earlier peak in community weighted spring activity (Figure S3). As we activated the traps before crop plant emergence, our results show that flea beetles are active in the field already before crop emergence, which leaves little time for plant protection. It is thus not surprising that prophylactic seed coatings with systemic insecticides are a standard practice in flea beetle management in Sweden and elsewhere (Tansey et al., 2009). Further, complementary foliar applications of insecticides against flea beetles are likely most effectively timed according to the degree of leaf injury to the seedlings (Lundin, 2020) rather than the activity and phenology of the flea beetles as explored here. The differences in activity windows among species do, however, have potential implications for insecticide resistance development and insecticide-induced assemblage shifts among sympatric flea beetle species (Ekbom & Müller, 2011; Tansey et al., 2008), as *P. vittula* and the *Chaetochnema* species will be less exposed to late foliar insecticide sprays in the crop. It is important to note that our monitoring dates in spring varied in the different fields depending on sowing dates and crop phenology. Activity peaks likely depend on crop phenology with for example limited activity in the field before the crop is sown. Therefore, in our analyses, we did not aim to establish any generalisation regarding what day of the year the different flea beetle species are most active, but rather to make relative comparisons between the activity peaks of the different species.

*Phyllotreta atra* had (together with *C. concinna*) the latest community weighted mean peak of summer emergence, which indicates that this species requires more accumulated degree-days for reproduction. *Phyllotreta atra* has been described as a drought-adapted species (Blunck, 1932) and was historically mainly reported from spring oilseed rape in the more southern, warmer regions in Sweden (Mühlow & Sylvén, 1953), while *P. undulata* had previously been predominant in the study region (Ekbom, 1990; Ekbom, 1991). In recent years, however, *P. atra* has been recorded in considerable numbers in the study region (Boetzl et al., 2023), providing proof that the species has extended the centre of its range northwards. Warmer and longer seasons in this region of Sweden due to climate change have likely promoted *P. atra* over other strictly specialised flea beetle species. *Phyllotreta vittula* emerged earlier than other species in summer, which reflects its earlier peak activity in spring and indicates that developmental times are rather constant for species other than *P. atra*.

All six selected species had similar spring emergence and single individuals of all species were found in the emergence traps already in the first week after trap activation in some fields. In Canada, where the introduced European species *P. striolata* and *P. cruciferae* are major pests on canola/spring oilseed rape, *P. striolata* was found to emerge and disperse earlier than *P. cruciferae* (Lamb, 1983; Turnock et al., 1987; Wylie, 1979). In our study, *P. striolata* tended to emerge earlier than the other species, but this difference was not significant, likely due to the generally low number of emerging *P. striolata* in the field margins (Table 1). As clear differences in spring emergence were absent, we find no necessity for predictive models for European flea beetle emergence to consider species identities in the flea beetle assemblage, although it should be noted that this conclusion is based on a single year of study.

## Basic biological information needed for effective flea beetle management

Effective pest management requires information about pest life cycles in order to target pest control precisely (Zalom, 1993). While our study adds to the knowledge of the life cycles and ecological preferences of different flea beetle species, many important knowledge gaps remain. In particular, we need improved understanding of the habitat use of the flea beetles, and how local conditions such as climate, crop management or the availability of certain habitats in both space and time, interact with their life cycles. In particular, the preferences for overwintering habitats should be assessed for each of the species using all potentially available habitats in a landscape, including wooded areas and the harvested oilseed rape fields. Additionally, effective dispersal radii of the species need to be estimated in order to choose a relevant spatial scale for pest management. As previous works have shown most effects of characteristics of the surrounding landscapes to be short ranged (0.5–1 km) in the flea beetle species studied here and in closely related species, the primary focus should be put within this range (Boetzl et al., 2023; Perez-Alvarez et al., 2018). Lastly, effective sustainable pest management strategies beyond the use of systemic insecticides, considering options such as entomopathogenic fungi and nematodes, pheromone-baited traps and the use of natural enemies such as generalist predators and specialised parasitic wasps (Ekbom, 1991; Wylie, 1988), need to be developed. These should be combined with other management strategies that have been shown to decrease flea beetle pest densities in spring oilseed rape, like no-till systems (Lundin, 2019). Among similar strategies, the use of entomopathogenic fungi (Price et al., 2024) or companion plants (Seimandi-Corda et al., 2024) has recently been shown promising as part of an integrated pest management strategy against the related cabbage stem flea beetle in winter oilseed rape (Ortega-Ramos et al., 2022). An incorporation of these missing aspects and a closer synchronisation of pest management strategies with the life cycles of flea beetle pests could allow effective integrated pest management and lead to a more sustainable and effective pest regulation across years.

## AUTHOR CONTRIBUTIONS

**Fabian A. Boetzl:** Data curation; formal analysis; investigation; visualization; writing – original draft; writing – review and editing. **Gerard Malsher:** Data curation; investigation; writing – review and editing. **Riccardo Bommarco:** Conceptualization; funding acquisition; investigation; project administration; resources; supervision; writing – review and editing. **Ola Lundin:** Conceptualization; data curation; funding acquisition; investigation; project administration; resources; supervision; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data available on request from the authors.

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## SUPPORTING INFORMATION

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

**Data S1.** Supporting information.

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