



Within-field overwintering contributes to arthropod predator assemblages in arable fields irrespective of tillage intensity

Janina Heinen^{a,b,*}, Monique E. Smith^{a,1}, Sara E. Emery^c, Ola Lundin^a,
Riccardo Bommarco^a

^a Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

^b Department of Agroecology Crop Health, Slagelse, Denmark

^c Department of Entomology, Cornell University, New York, United States

ARTICLE INFO

Keywords:

Emergence
Direct seed
Reduced tillage
Community assembly
Agroecosystem
Soil disturbance
Herbivores
Crop protection
Diversified agriculture
Conservation biological control

ABSTRACT

Arthropod predators and pests overwinter in arable fields, but little is known about predator and pest overwintering under contrasting tillage intensities. Further, the contribution of within-field overwintering predator communities to the overall ground dwelling community is understudied. We sampled arthropod predators (carabids, staphylinids and spiders) and pests overwintering in arable fields, and estimated the activity densities of overall ground dwelling predator communities from early spring until harvest 2021. We sampled 29 conventionally managed crop fields managed using no till (direct drill), reduced tillage (non-inversion) or inversion tillage between harvesting winter cereals and sowing winter oilseed rape in 2020. No till management resulted in higher species diversity of overwintering predators, compared with inversion tillage. Tillage effects on density of overwintering predators and pests depended on sampling time. Predator and pest emergence were higher under inversion tillage compared with no till early in the season. During mid and late season, predator emergence was higher under reduced tillage compared with no till and inversion tillage. Tillage had no effects on species richness but affected community composition (beta-diversity) of the overwintering predator communities. Overwintering and overall ground dwelling predator communities were distinctly different in early season and homogenised as the crop-growing season progressed. The high average density of predators emerging per m² of arable soil within the fields, 108 carabids, 604 staphylinids and 56 spiders, emphasises the need to adapt arable management in order to support arthropod overwintering in crop fields for enhanced biological pest regulation.

1. Introduction

Abundant and diverse arthropod predator communities can suppress arthropod pest populations in arable crop fields (Cardinale et al., 2003; Dainese et al., 2019). Managing the crop field such that the diversity and abundance of arthropod predators is enhanced can improve biological regulation of crop arthropod pests (Cardinale et al., 2003; Letourneau et al., 2009). Successful management of arthropod predator communities aligns with the ecological requirements of the predators across their life stages (Rowen et al., 2020; Tooker et al., 2020).

Although arable fields are often considered unsuitable for overwintering, reducing the intensity of crop management can enhance overwintering of arthropod predator communities within the field (Holland et al., 2009; Hanson et al., 2017). This is particularly important

in landscapes of high simplification, where improvement of local conditions within the crop field mitigates the lack of other suitable overwintering habitats in the landscape (Sarthou et al., 2014; Tamburini et al., 2016; Sutter et al., 2018). The contribution of within-field overwintering to overall assembled communities of arthropod predators in arable fields needs to be further explored, especially under contrasting crop management regimes (Wilby and Thomas, 2002), to identify practices that support abundant and diverse communities (Holland et al., 2009; Hanson et al., 2017).

Within-field management, such as tillage negatively impact arthropod predators by causing the direct mortality of pupae, larva and adults, and by indirectly changing soil structure and the availability of resources (Thorbeck and Bilde, 2004; Shearin et al., 2007; Mesmin et al., 2020). Tillage can impair habitat features that have been shown to

* Corresponding author at: Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden.

E-mail address: Janina.heinen@slu.se (J. Heinen).

¹ Co-first authors

increase overwintering in arable fields, such as high soil moisture (Kober et al., 2024) and continuous vegetation cover (Dennis et al., 1994; Clem and Harmon-Threatt, 2021). Reducing tillage intensity or adopting no till practices can increase arthropod predator overwintering success compared with inversion tillage (Pfiffner and Luka, 2000; Ullmann et al., 2016), but effects on arthropod predators vary across species groups under contrasting tillage regimes (Hanson et al., 2015). Unfortunately, reduced intensity tillage practices might also increase survival of crop pests that overwinter in the field (Rowen et al., 2020). Effects of reduced tillage intensity on within-field overwintering for arthropod predators and pests in conventionally managed fields remain unclear.

Creating suitable habitats within fields for arthropod overwintering can strengthen biological pest control, as predator communities that are present early in the season are more effective at suppressing herbivores throughout the cropping season (Costamagna et al., 2015; Jonsson et al., 2017; Tortosa et al., 2022). Early within-field emergence contributes to the establishment of predator communities, suppressing outbreaks of pest populations (Ramsden et al., 2015). To advance the understanding of how overwintering communities contribute to pest control, we need to explore whether factors that create favourable microclimatic conditions, such as remaining plant residue and reduced soil disturbance in non-tilled arable fields, promote arthropod overwintering compared with inversion-tilled fields (Ganser et al., 2019; Litovska et al., 2025).

Temporal variation in resource availability within and outside arable fields, as well as species phenology across the crop growing season, shape the spatiotemporal dynamics of predators and their colonisation of arable fields (Holland et al., 2005; Rand et al., 2006; Welch and Harwood, 2014). Effects of tillage intensity on within-field community assembly would therefore need to be complemented with examinations of overall assembled predator communities in crop fields and across the season (Lichtenberg et al., 2017). Direct comparisons between overwintering and overall assembled communities are challenging due to the inherent differences in sampling methods (Knapp et al., 2020; Djoudi et al., 2019; Hanson et al., 2016). Such comparisons are, however, necessary if we want to understand the contribution of predator spill-over from adjacent habitats into fields (Rand et al., 2006; Clem and Harmon-Threatt, 2021), as well as the role of within-field emergence in assemblage and functioning of predator communities.

We sampled arthropods with emergence traps and pitfall traps across fields with three levels of tillage intensity: no till (direct drill), reduced tillage (non-inversion), and inversion tillage. This allowed us to track the legacy effect of soil tillage on the overwintering success of predators and pests via their emergence, and the contribution of within-field overwintering to the overall ground dwelling predator communities the subsequent year. We expected the density of overwintering predator communities (H1a) as well as pest density (H1b) to gradually decrease as tillage intensity increased. Accordingly, we expected the overwintering community composition to differ among treatments, reflecting the predator assemblages' response to tillage disturbance, with more diverse communities persevering and overwintering in lesser-disturbed fields (H2). Further, we expected overwintering predator communities to be more similar to overall ground dwelling predator communities in the less disturbed fields (H3), as these assemblages should be determined by within-field community build-up of abundant and diverse overwintering communities. In more highly disturbed fields, we instead expected immigration to play a greater role in shaping the predator communities, leading to greater dissimilarity between overwintering and overall communities. We expected communities of overwintering predators and overall ground dwelling predator communities to become more homogenised as the crop season progresses (H4), as overwintering predators gradually integrate into the overall ground dwelling communities.

2. Material and method

2.1. Field selection and set up

We initially selected 30 conventionally managed fields, 10 each of the three tillage treatments: no till, reduced tillage and inversion tillage in Västra Götaland County, Sweden (Fig. A1). Minimum and maximum distances between fields was 0.4 and 53 km, respectively. Emergence traps were continuously destroyed by wildlife in one field subjected to no till and we therefore excluded this field from all further analysis. All fields were sown with winter cereals in autumn 2019, 28 with winter wheat (*Triticum aestivum*), and one with winter barley (*Hordeum vulgare*). Tillage was implemented in-between harvest of winter cereals in late July 2020 and seeding of winter oilseed rape (*Brassica napus*) in early to mid-August 2020 (Table A1). Winter oilseed rape was harvested in August 2021. Inversion tillage fields were managed with mouldboard ploughing, reduced tillage was characterised by non-inversion tillage of the soils with various disc and tine cultivators, and in no till fields farmers used either direct drill or a seed drill on a subsoiler.

To assess changes in habitats after tillage, we quantified the remaining plant residue on the soil surface after seeding of winter oilseed rape. Residue cover was assessed as percentage soil coverage within a 60 by 60 cm sampling area, with three replications per field. Residue cover was assessed in 10 % increments. Plant residue cover increased with decreasing intensity of tillage, showing highest plant cover under no till, intermediate plant cover under reduced tillage and lowest plant cover under inversion tillage (Fig. A2).

We calculated the amount of arable land, forest and semi natural habitat (permanent pastures and other open habitats with vegetation) in a 1 km radius around each field site based on digital land cover maps (Terrängkartan, Lantmäteriet, 2018), and Integrated Administration and Control System & Nationella marktäckedata (Naturvårdsverket, 2020). Fields were generally embedded in landscapes dominated by arable land. On average, fields had 83.67 ± 15.28 % of arable land cover in a 1 km buffer around the field sites with a minimum and maximum percentage of 32.41 %; and 98.72 % respectively. Landscape elements were balanced across fields with the three tillage treatments (Table A2). In each field, a 24 by 24 m area located at the border of the field was established in which no insecticides were applied. Herbicide and fungicide applications were performed according to farmer discretion. To avoid effects from insecticide spray drift on community assessments, sampling took place in a 12 by 12 m sampling area centrally located within the unsprayed area.

2.2. Overwintering predator and pest community sampling

In early spring 2021 (25th – 27th of March), we set up emergence traps prior to the activity period of overwintering arthropods. Overwintering communities of carabids, staphylinids, spiders and herbivorous insects that can be crop pests, particularly for oilseed rape, were sampled from the end of March until the end of July 2021 (Table A3). Carabids and spiders were identified to species and staphylinids were identified to genera. A list of arthropod pests included in the assessment is provided in Table A4. The emergence traps consisted of a metal ring (diameter 35 cm, 30 cm height) covering 0.096 m² of soil each. The metal ring was buried 10–15 cm deep into the soil to prevent immigration and emigration from the sampling area. Emergence traps were sealed with a fine mesh and secured with a belt around the metal ring (Fig. A3). Vegetation within the metal ring was continuously trimmed so it would not outgrow and damage the emergence traps. We captured overwintering individuals fortnightly using a pitfall trap (11.5 cm diameter, 10 cm depth) located within the metal ring for a total of seven sampling sessions. The pitfall trap was filled with approx. 200 ml of a mix of water and odourless detergent at the beginning, and again after each sampling. We placed three pairs of traps per field at 12 m from and parallel to the field edge, for a total of six emergence traps per field. Pairs

of traps were spaced approximately 2 m apart, and traps within pairs approximately 0.3 m apart. Overwintering arthropods were collected from a total surface area of 0.57 m² per field per sampling session.

2.3. Overall ground dwelling predator community sampling

We assessed the activity density of ground dwelling predator communities in the open fields using pitfall trapping at three occasions in, May, June and July 2021. Each field had five pitfall traps (11.5 cm diameter, 10 cm depth), filled with approx. 200 ml of a mix of water and odourless detergent. Pitfall traps remained open for four consecutive days. All collected carabids, staphylinids and spiders were stored in 70 % ethanol until identification. Carabids and spiders were identified to species and staphylinids were identified to genera. The activity density for each predator community was then calculated as the total number of individuals (carabids, staphylinids and spiders combined) caught per trap and sampling round.

2.4. Statistical analysis

All analyses and visualisations of results were done in R version 4.3.1 (R core Team, 2023). We analysed the data using three approaches. Firstly, we compared the densities of predators and pests and within-field diversities of predators between tillage treatments (2.4.1). Secondly, we compared the predator community composition between fields within the three tillage treatments (2.4.2). Finally, to explore the contribution of locally overwintering predator communities to overall ground dwelling predator communities in fields we compared the species present in these two communities in each tillage treatment (2.4.3).

2.4.1. Density and within-field diversity

Some emergence traps (12 out of 609 traps; 1.9 %) were destroyed during the season (see Table A3). To account for this variation in sampling effort, we used the mean density of individual arthropods per trap pair in each field and sampling session for all analysis. Thus, we compared the effects of tillage treatments on the mean densities per trap of overwintering predators and pests over the growing season. The observed species richness of overwintering predators was calculated as the number of individual species, whereas predator species diversity was calculated using Shannon's diversity index, which incorporates both species richness and the mean density of each species to account for the evenness of the communities (Shannon, 1948).

We built models to assess the impact of tillage on each response variable, i.e., the average density for both predator and pests overwintering, and species richness and species diversity of overwintering arthropod predators, over the growing season. Each model had the main effect of tillage treatment, no till, reduced tillage and inversion tillage, and time, included as a continuous variable calculated as the number of days since the deployment of the first trap, and their interaction. We modelled the temporal trend using cubic B-splines with the optimal degrees of freedom determined by multiple metrics, including Akaike information criterion (AIC), Bayesian information criterion (BIC) and likelihood ratio tests, comparing models with degrees of freedom ranging from 3 to 6. The model was selected when at least two of the metrics were in agreement and the simplest model was favoured when delta AIC was less than 2 between different models (Table A5). We accounted for multiple samplings across the season by setting field as a random effect in each model and models were adjusted for the best fit of the data based on "DHARMA" version 0.4.6 (Hartig, 2022) which checks residuals, assesses zero-inflation, tests for outliers, and evaluates dispersion. Therefore, the final models for mean density of both predators and pests (rounded up to the nearest integer) were generalised linear mixed models with a negative binomial distribution, which were fitted using the package "glmmTMB" version 1.1.7 (Brooks et al., 2017). Species diversity and richness were analysed using linear mixed models in the package "lme4" version 1.1.34 (Bates et al., 2015) with a Gaussian

distribution. Species richness needed to be square root transformed to meet model assumptions. We employed a hierarchical hypothesis testing approach, first using Type III Wald chi-square tests to evaluate the tillage by time interaction, and upon finding no significant interaction, proceeding to Type II tests for assessing main effects. Pairwise comparisons between tillage treatments were performed using estimated marginal means with Tukey's adjustment for multiple comparisons. Model fit was evaluated using Nakagawa's R² values to quantify variance explained by fixed effects alone and the entire model including random effects (Nakagawa et al., 2017).

2.4.2. Predator community composition

To assess differences among tillage treatments in the community composition i.e., both richness and density, of overwintering predator communities, we first removed the sampling session effect by examining the total emerged community per field (but see Table A6 for models with sampling session included). To statistically test for differences among tillage treatments, we calculated differences among fields using Bray Curtis dissimilarity and then visualised with Principal Coordinate Analysis (PCoA) plots. We then tested for tillage treatment effects with a Permutational Multivariate Analysis of Variance (PERMANOVA) with *adonis2* in the "vegan" package (version 2.6–4, Oksanen et al., 2022) with 9999 permutations. Pairwise comparisons of each group were evaluated with *pairwise.adonis* using a false-discovery rate correction for multiple tests. We evaluated differences between sample variability using homogeneity of multivariate dispersions tests (*betadisper*), followed by ANOVAs to compare the mean distance-to-centroid. Pairwise dispersion comparisons were carried out using Tukey's *post-hoc* significant differences.

2.4.3. Overwintering and overall ground-dwelling communities

The densities of individuals from the emergence traps (area-based sampling) and open pitfall traps (activity-based sampling) could not be directly compared due to the different sampling techniques, so we transformed the density information to presence or absence of species. We also only compared the emergence traps that were set up either directly before or at the same time as each pitfall trap, giving three comparable sampling months of May, June and July to track seasonal effects. Sample differences between emergence and pitfall traps were calculated using a Jaccard dissimilarity matrix for presence-absence data and visualised with PCoA plots. The Jaccard dissimilarity matrix was also used for PERMANOVA to test for differences between tillage treatments, sampling month, community sampled (based on the trap type) and their interactions. Field was included as a random effect to account for multiple testing over the season. We evaluated differences between sample variability in the same way as for the overwintering communities above.

3. Results

3.1. Abundance and diversity of overwintering predator and pest communities

Over the entire sampling period from March to August, we caught 11572 individuals belonging to 89 species of arthropod predators, and 3957 individuals belonging to 18 species of arthropod pests. Staphylinids were the most abundant predator group making up 78 % of individuals and 25 % of species, followed by carabids (14 % of individuals and 42 % of species) and spiders (8 % individuals and 34 % of species, Figure A4). Cumulative sums averaged across fields' show that 108 ± 80 carabids, 604 ± 396 staphylinids and 56 ± 32 spiders overwintered per m² of arable soil (Figure A5).

The emergence of overwintering predator community in the fields increased in density, richness and diversity over the season, peaking in all three in late June, 74 days after the first trap was deployed (Fig. 1). The effect of tillage on predator density depended on sampling session

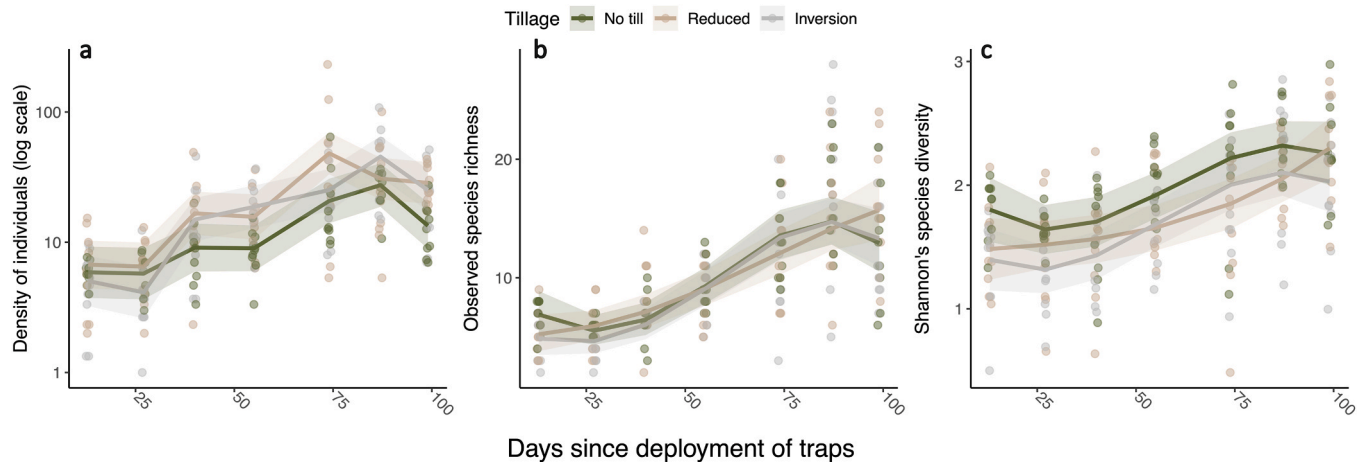


Fig. 1. Density and within-field species richness and Shannon diversity of overwintering arthropod predator communities over the growing season between April and July. Density is represented as the mean number of individuals per 0.192 m² and field (a), followed by observed species richness (b) and Shannon's species diversity (c) per field. Lines are the model estimated means and the 95 % confidence intervals are indicated by the shaded areas. Colours represent tillage treatments and dots represent mean values per field.

Fig. 1a, ANOVA $p = 0.027$; Table 1). There were no differences in density of emerging predators between tillage treatments until the second sampling on day 55, whereby density in inversion tillage was higher than no till (Tukey, $p = 0.025$; 18.7 ± 3.6 and 9 ± 1.9 individuals per 0.192 m², respectively). At day 74, reduced tillage had the highest density (48 ± 9.1 individuals per 0.192 m²) compared with no till (Tukey, $p = 0.006$; 20.7 ± 4.2 individuals per 0.192 m²) and inversion tillage (Tukey, $p = 0.040$; 25.2 ± 4.8 individuals per 0.192 m²). There were no differences again until day 99, where the density was again higher in reduced tillage (28.6 ± 5.4 individuals per 0.192 m²) than no till (Tukey, $p = 0.018$; 13.4 ± 2.8 individuals per 0.192 m²). Tillage treatment had no impact on the observed species richness of predator communities (ANOVA, $p = 0.732$, Fig. 1b, Table 1), but there was an effect on Shannon's species diversity (ANOVA, $p = 0.032$, Fig. 1c). *Post-hoc* tests among tillage treatments for Shannon's species diversity showed that no till was higher than reduced tillage at day 74 (Tukey, $p = 0.037$; 2.2 ± 0.1 and 1.9 ± 0.1 , respectively). The other comparisons showed no significant differences.

The density of emerging arthropod pests was highest from late May and until the end of June (55–87 days after deployment of the traps) and there was a significant interaction between days and tillage treatment (Fig. 2, ANOVA, $p = 0.003$; Table 1). *Post-hoc* comparisons between the tillage treatments showed higher pest densities under inversion tillage compared to no till at day 55 (Tukey, $p = 0.005$; 9 ± 1.5 and 4.1 ± 0.8 individuals per 0.192 m², respectively) and day 74 (Tukey, $p = 0.019$; 23 ± 3.9 and 11.8 ± 2.2 individuals per 0.192 m², respectively). Tillage treatment comparisons during other sampling sessions were non-significant.

Beta-diversity of overwintering predator communities differed among tillage treatments (Fig. 3). No till and inversion tillage had partially distinct species composition, whereas communities in reduced

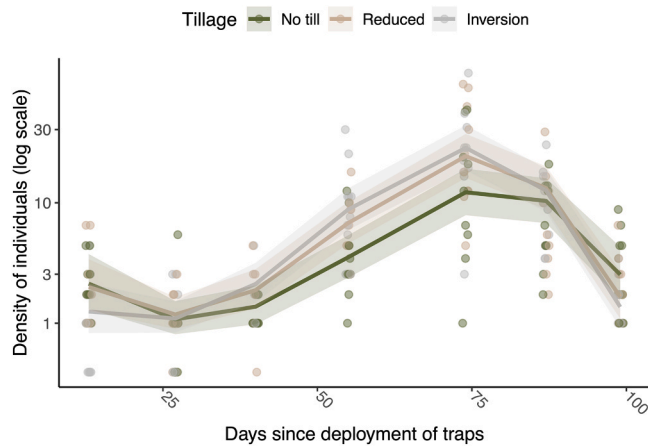


Fig. 2. Mean density of crop pest individuals emerging per 0.192 m² and field over the growing season between April and July. Lines are the model estimated means and the 95 % confidence intervals are indicated by the shaded areas. Colours represent tillage treatments and dots represent raw data collected in each field.

tillage were similar to both no till and inversion tillage (Table 2). Overall, communities were characterised by a large core group of predators occurring across all tillage treatments.

Table 1

Results from Analysis of Variance (ANOVA) with Type II or III Wald chi-square tests for assessing the main effects of days since deployment of traps and tillage and their interaction. Type II Wald chi-square tests is reported for models without significant interaction to assess main effects. Type III test is reported for models with significant interaction.

	Predator density			Observed species richness			Shannon's species diversity			Pest density		
	χ^2	df	P value	χ^2	df	P value	χ^2	df	P value	χ^2	df	P value
Intercept	58.49	1	< 0.001							10.72	1	0.01
Tillage (T)	0.87	2	0.64	0.62	2	0.73	6.86	2	0.03	2.48	2	0.28
Days (D)	59.97	6	< 0.001	307.89	3	< 0.001	121.28	3	< 0.001	82.71	3	< 0.001
T:D	23.05	12	0.03	8.94	6	0.18	7.15	6	0.31	19.64	6	0.003
R2 marginal		0.621			0.557			0.364			0.699	
R2 conditional		0.711			0.647			0.506			0.787	

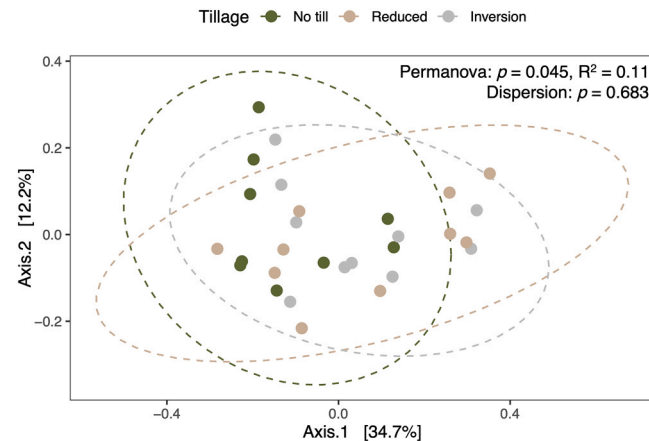


Fig. 3. The emerging arthropod predator community composition according to Principal Coordinate Analysis (PCoA). Points represent the predator community found in each field over the entire season coloured by tillage treatment. The placement of points is based on an Euclidean measure of Bray–Curtis dissimilarities among the fields, whereby points closer together are more similar in the species present and their densities than points further away. Ellipses represent the 95 % confidence level. PERMANOVA results based on the same dissimilarity matrix with tillage treatment as a main effect are presented.

Table 2

Pairwise comparison (PERMANOVA) of overwintering arthropod predator community composition between tillage treatments (no till, reduced and inversion tillage) based on Bray–Curtis dissimilarity. Presented are degrees of freedom (df), sums of squares (SS), pseudo F-, R-squared as well as p-, and adjusted p-values after correcting for multiple tests using the false-discovery rate correction.

Tillage pairs	df	SS	Pseudo-F	R ²	p	p-adjust
No till vs Inversion	1	0.259	2.101	0.105	0.022	0.065
No till vs Reduced	1	0.229	1.723	0.087	0.074	0.111
Inversion vs Reduced	1	0.117	1.063	0.056	0.335	0.335

3.2. Comparison of overwintering and overall ground dwelling predator communities

In total, we collected 41694 individuals from 166 species of overall ground dwelling arthropod predators using open pitfall traps. The most abundant predator group was carabids, which made up 46 % of individuals and 37 % of species, followed by staphylinids (28 % of individuals and 15 % species) and spiders (26 % individuals and 46 % of species). However, to compare with emergence traps all densities were converted to presence absence of species to account for the different trapping methods (see methods).

The composition of species in overwintering and overall ground dwelling predator communities differed throughout the season (Fig. 4). Using PERMANOVA with Jaccard distance of the species presence in each field, we found an interaction between the type of predator community and sampling month (Table 3), where the overwintering and overall ground dwelling predator communities became more similar as the season continued. To explore this interaction, we ran separate PERMANOVA models for each month using only predator community type as a response variable. The communities were more similar between overwintering and overall ground dwelling predators later in the season as demonstrated by a weakening of R² values from May to June and July (R² = 0.27, 0.20, 0.19 respectively) and supported by the PCoA (Fig. 4). Tillage treatment did not affect the relationship between overwintering and overall ground dwelling predator communities but there was an overall effect of tillage (Table 3; Fig. 4). Pairwise comparisons resembled the trend in the overwintering communities where there was a significant difference between no till and inversion tillage (p-

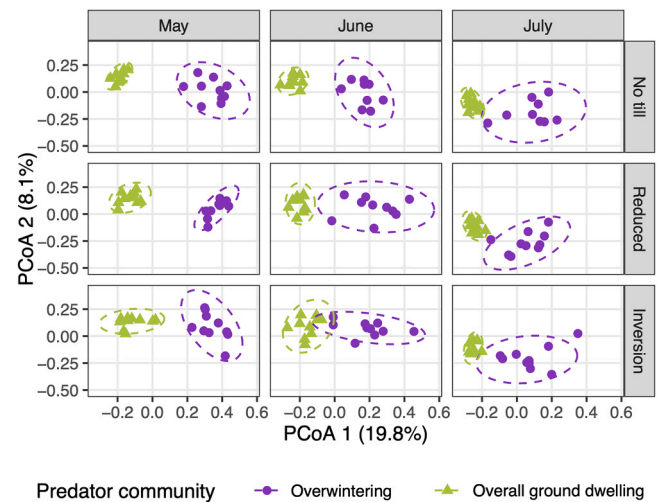


Fig. 4. Overwintering and overall ground dwelling predator communities in the tillage treatments of no till, reduced and inversion tillage, and over the sampling months according to Principal Coordinate Analysis (PCoA). Points represent the predator community found in each field, per sampling month and trap type (emergence trap: purple circle, or open pitfall trap: green triangle). The placement of points is based on a Jaccard dissimilarity matrix for presence or absence data whereby points closer together are more similar in the presence of predator species than points further away. Ellipses represent the 95 % confidence level of each grouping (tillage treatment x sampling month x type of predator community).

Table 3

Results of PERMANOVA based on Jaccard dissimilarity of predator communities. Main effects included tillage treatments (T), sampling month (SM) and the type of predator communities (C, overwintering or overall ground dwelling) and their interactions. Presented are degrees of freedom (df), sums of squares (SS), pseudo F-, R-squared as well as p-, and adjusted p-values after correcting for multiple tests using the false-discovery rate correction. Significant differences (p < 0.05) in bold.

	df	SS	Pseudo-F	R ²	p
Tillage (T)	2	0.971	0.0202	2.4999	0.001
Sampling month (SM)	2	4.613	0.09601	11.8804	0.001
Community sampled (C)	1	7.558	0.15728	38.9259	0.001
T:SM	4	0.672	0.01397	0.8646	0.741
T:C	2	0.536	0.01115	1.3798	0.09
SM:C	2	2.077	0.04322	5.3482	0.001
T:SM:C	4	0.755	0.01571	0.9722	0.492
Residual	159	30.872	0.64245		
Total	176	48.054	1		

adjusted = 0.019) and no other differences were significant.

4. Discussion

We found on average 108 ± 80 carabids, 604 ± 396 staphylinids and 56 ± 32 spiders emerging per m² of arable field over the season (Figure A4, A5). These numbers are comparable to other findings in crop fields (Hanson et al., 2017; Djoudi et al., 2019; Boetzel et al., 2022), and illustrate the importance of within-field habitats for arthropod predator communities. Contrary to our expectation (H1a), differences in predator communities were subtle across tillage treatments, with no overall decrease in overwintering communities with increasing tillage intensity. We suggest that the tillage timing likely contributed to the similarity in overwintering densities of predators across treatments. Tillage in late summer or autumn can be less detrimental for many ground dwelling predator species compared with tillage in spring, as mobile and active adult predators can partly avoid the disturbance in autumn (Holland and Reynolds, 2003). Consequently, early autumn sowing of winter oilseed

rape can increase the number of arthropod predators overwintering compared with in spring sown crops, by lessening the impact on larvae and eggs in the soils (Roger-Estrade et al., 2010; Sutter et al., 2018). However, the effects of tillage timing on carabids are unclear, as many species have extended breeding periods (Fadle and Purvis, 1998; Hance, 2002).

The effect of tillage on overwintering densities of arthropod predators depended on the time of sampling, with higher density of emerging predators in inversion tillage fields early in the season. Higher densities under inversion tillage can be linked to earlier warming of inverted soils (Soane et al., 2012). In the middle of the season, and during peak emergence, reduced tillage had the highest density of emerging predators compared with both no till and inversion tillage. The increase in emerging individuals under reduced tillage might be linked to some species that are well adapted to disturbances and their relative increase in density in fields. Carabid beetles can benefit from recent soil disturbance (Boetzl et al., 2022), but the mechanisms explaining this are not understood and we found no effects when predator groups were analysed separately (Fig. A6, Table A7). In reduced-tilled fields, the combination of remaining plant residue, greater soil moisture and higher late season activity density could increase the ovipositing, leading to increased densities of overwintering predators compared to inversion tillage (Holland et al., 2007; Kober et al., 2024). How contrasting tillage managements can provide the same relative outcome for overwintering communities needs further investigation with a focus on the specific habitat conditions, tillage timing, and combined assessments of oviposition rate and emergence after winter.

We expected greater diversity of arthropod predator communities in undisturbed field under no till compared to reduced and inversion tillage (H2). Partly in line with this hypothesis, Shannon's species diversity of overwintering arthropod predator communities, but not the observed species richness, was higher under no till compared with inversion tillage. As Shannon's species diversity integrates species richness (which was not affected by tillage treatment) and relative abundances across the species, our results indicate that overwintering communities in no till fields are more even, whereas in tilled fields, communities might be dominated by few or single species coping well with disturbance. The increased amount of plant residue on the soil surface under reduced and no tillage, could create favourable microclimatic conditions buffering soils against desiccation, increase soil moisture and thus benefit overwintering predator communities (Dennis et al., 1994; Kober et al., 2024). Such benefits could allow more diverse and even communities to establish in the no till fields with greater niche availability and habitat stability. Diverse predator communities are not only more resilient but can, through exploitation of a greater variety of prey, increase their biological regulation of pests (Schneider et al., 2016; Daines et al., 2017).

Contrary to our expectation, we observed no overall difference in insect pest emergence between tillage treatments (H1b), although pest emergence was higher under inversion tillage than no till in two sampling sessions in late spring. We had anticipated greater pest densities in fields under no till compared to inversion tillage (H1b) due to less physical disruption of overwintering pests in this treatment. However, more diverse predator communities under no till might have more effectively controlled pest larvae in the soil (Zaller et al., 2009), or adult pest arthropods before overwintering in autumn. In this study, the relative contribution of physical destruction of overwintering pests, and pest control through arthropod predators on pest emergence in the following year cannot be disentangled. Further targeted research is needed to assess role of physical pest reduction through tillage and the influence of abundant and diverse ground dwelling predators on overwintering pest populations in arable fields.

Overwintering predator communities were not more similar to overall ground dwelling predator communities in the less disturbed fields as we expected (H3). Instead, we found that most arthropod predator species belong to a core group of highly overlapping species,

with similar overlap of overwintering and overall ground dwelling communities across tillage treatments. Legacies of previous management, filtering for species that are well adapted to disturbances in regularly disturbed arable fields (Smith and Mortensen, 2017) could lead to uniform communities over time. While we only investigated the effect of a single tillage event, we suspect community differences to become more accentuated when comparing low and high intensity tillage across multiple seasons, especially in simplified arable landscapes with overall high soil disturbance and a lack of natural overwintering habitat (Tamburini et al., 2016). Over several seasons, repeated disturbance could shift trait compositions within predator communities to favour traits associated to high disturbance, e.g. more mobile macropterous over brachypterous insects (Hanson et al., 2017). Because we only investigated a single tillage event and also did not have complete information on the field management history, other management such as the history of tillage and crops grown beyond the pre-crop could also have affected the communities seen in these fields. Tracking the overwintering communities across several seasons, crop changes, and in conjunction with functional assessment of species communities could further inform the effect of management on overwintering communities in the longer term.

In line with our last hypothesis, we found distinct early season communities, trapped by pitfalls (i.e. overall ground dwelling) and with emergence traps (i.e. overwintering) that gradually became more similar as the season continued (H4). Differences in these communities caught over the season, suggest benefits for early community build-up via locally emerging-overwintering predators. These emerging-overwintering communities, could strengthen ecosystem functioning early in the season and reduce pest damages throughout the season (Macfadyen et al., 2015; Heinen et al., 2024). However, comparisons of the relative importance of overall ground dwelling and emerging-overwintering communities for assemblages is challenging due to the inherent differences in sampling methods used to assess communities. While the number of trapped individuals for pitfall traps depend on the combination of activity and density of arthropods on the ground surface, emergence traps estimate the density per unit area based on soil dwelling life stages that emerge in spring. Pitfalls might therefore underestimate the density and diversity of small species with lower dispersal ability compared with larger bodied arthropods (Luff, 1975; Knapp et al., 2020; Ahmed et al., 2023). Although this might introduce bias for comparing abundances between emerging and overall populations within fields, it is still possible to compare relative differences in emerging and overall communities between fields and management treatments. We minimised risk of bias by only using presence or absence of species, and not densities, when comparing pitfall with emergence trap catches. Furthermore, we dug the emergence traps to the depth of 10–15 cm which is in line with what other researchers have done (e.g. Roume et al., 2011; Mestre et al., 2018; Ganser et al., 2019). We found that pitfall and emergence traps capture a distinct community of arthropod predators. It is, however, possible that some predators were able to dig themselves into the closed emergence trap area without necessarily having overwintered within the field. We encourage further experimentation with emergence traps using varying burying depths to explore if this is the case and suggest a standard.

We find about half the species in overall communities were emerging within the field. This suggests that a considerable proportion of arthropod predator biodiversity is sustained through overwintering within arable fields (Djoudi et al., 2019), underlining the need to understand how within-field management affects arthropod ecology and their community build up. Beyond tillage, other management practices such as crop rotation and fertilisation regimes affect the overwintering of arthropod predators. Management that supports biodiversity and ecosystem services can only be adapted efficiently if we understand species' ability to overwinter in crop fields versus their colonisation rate from outside fields and non-crop habitats.

CRediT authorship contribution statement

Janina Heinen: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Monique E. Smith:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Sara E. Emery:** Writing – review & editing, Methodology, Conceptualization. **Ola Lundin:** Writing – review & editing, Resources, Conceptualization. **Riccardo Bommarco:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Funding

This work was supported by senior career funding from the Faculty of Natural Resources and Agricultural Sciences at the Swedish University of Agricultural Sciences, awarded to Riccardo Bommarco.

Declaration of Competing Interest

All authors declare no conflict of interest.

Acknowledgements

We thank the farmers that granted us access to their fields. We thank Gerard Malsher for sample processing and species identification, and all field assistants for the data collection.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.109822](https://doi.org/10.1016/j.agee.2025.109822).

Data availability

Data is available at: 10.5281/zenodo.15680006.

References

- Ahmed, D.A., Beidas, A., Petrovskii, S.V., Bailey, J.D., Bonsall, M.B., Hood, A.S.C., Byers, J.A., Hudgins, E.J., Russell, J.C., Růžicková, J., Bodey, T.W., Renault, D., Bonnaud, E., Haubrock, P.J., Soto, I., Haase, P., 2023. Simulating capture efficiency of pitfall traps based on sampling strategy and the movement of ground-dwelling arthropods. *Methods Ecol. Evol.* 14, 2827–2843. <https://doi.org/10.1111/2041-210X.14174>.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Boetzel, F.A., Krimmer, E., Holzschuh, A., Krauss, J., Steffan-Dewenter, I., 2022. Arthropod overwintering in agri-environmental scheme flowering fields differs among pollinators and natural enemies. *AGEE* 330, 107890. <https://doi.org/10.1016/j.agee.2022.107890>.
- Brooks, M.E., Kristensen, K., Benthem, K.J., van, Berg, C., W, Magnusson, A., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9 (2), 378. <https://doi.org/10.32614/RJ-2017-066>.
- Cardinale, B.J., Harvey, C.T., Gross, K., Ives, A.R., 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecol. Lett.* 6 (9), 857–865. <https://doi.org/10.1046/j.1461-0248.2003.00508.x>.
- Clem, C.S., Harmon-Threalt, A.N., 2021. Field borders provide winter refuge for beneficial predators and parasitoids: a case study on organic farms. *J. Insect Sci.* 21 (3), 2. <https://doi.org/10.1093/jisesa/ieab027>.
- Costamagna, A.C., Venables, W.N., Schellhorn, N.A., 2015. Landscape-scale pest suppression is mediated by timing of predator arrival. *Ecol. Appl.* 25 (4), 1114–1130. <https://doi.org/10.1890/14-1008.1>.
- Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalho, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Tschamrtke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S., Bezerra, A.D.M., Bianchi, F.J.J.A., Boreux, V., Bretagnolle, V., Caballero-Lopez, B., Cavigliasso, P., Cetković, A., Chacoff, N.P., Classen, A., Cusser, S., da Silva e Silva, F.D., de Groot, G.A., Dudenhöffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C., Hipólito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Keasar, T., Kim, T.N., Kishinevsky, M., Klatt, B.K., Klein, A.-M., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Liere, H., Maas, B., Mallinger, R.E., Martinez Pachon, E., Martínez-Salinas, A., Meehan, T.D., Mitchell, M.G.E., Molina, G.A.R., Nesper, M., Nilsson, L., O'Rourke, M.E., Peters, M.K., Plečá, M., Potts, S.G., Ramos, D. de L., Rosenheim, J.A., Rundlöf, M., Rusch, A., Sáez, A., Scheper, J., Schleuning, M., Schmack, J.M., Sciligo, A.R., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Sutter, L., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Willcox, B.K., Wratten, S.D., Yoshioka, A., Zaragoza-Trello, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. *Sci. Adv.* 5, eaax0121. <https://doi.org/10.1126/sciadv.aax0121>.
- Dainese, M., Schneider, G., Krauss, J., Steffan-Dewenter, I., 2017. Complementarity among natural enemies enhances pest suppression. *Sci. Rep.* 7 (1), 8172. <https://doi.org/10.1038/s41598-017-08316-z>.
- Dennis, P., Thomas, M.B., Sotherton, N.W., 1994. Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *JAE* 31 (2), 361. <https://doi.org/10.2307/2404550>.
- Djoudi, E.A., Plantegenest, M., Aviron, S., Pétilon, J., 2019. Local vs. landscape characteristics differentially shape emerging and circulating assemblages of carabid beetles in agroecosystems. *AGEE* 270–271, 149–158. <https://doi.org/10.1016/j.agee.2018.10.022>.
- Fadl, A., Purvis, G., 1998. Field observations on the lifecycles and seasonal activity patterns of temperate carabid beetles (Coleoptera: Carabidae) inhabiting arable land. *Pedobiologia* 42, 171–183.
- Ganser, D., Knop, E., Albrecht, M., 2019. Sown wildflower strips as overwintering habitat for arthropods: effective measure or ecological trap? *AGEE* 275, 123–131. <https://doi.org/10.1016/j.agee.2019.02.010>.
- Hance, T., 2002. Impact of cultivation and crop husbandry practices. In: Holland, J.M. (Ed.), *The Agroecology of Carabid Beetles*. Intercept, Andover, pp. 231–250.
- Hanson, H.I., Birkhofer, K., Smith, H.G., Palmu, E., Hedlund, K., 2017. Agricultural land use affects abundance and dispersal tendency of predatory arthropods. *BAAE* 18, 40–49. <https://doi.org/10.1016/j.baae.2016.10.004>.
- Hanson, H.I., Palmu, E., Birkhofer, K., Smith, H.G., Hedlund, K., 2016. Agricultural Land Use Determines the Trait Composition of Ground Beetle Communities. *PLoS* 11, e0146329. <https://doi.org/10.1371/journal.pone.0146329>.
- Hanson, H.I., Smith, H.G., Hedlund, K., 2015. Agricultural management reduces emergence of pollen beetle parasitoids. *AGEE* 205, 9–14. <https://doi.org/10.1016/j.agee.2015.03.001>.
- Hartig, F., 2022. DHARMa: residual diagnostics for hierarchical (Multi-Level /Mixed) regression models. R. Package Version 0 4, 6. <https://CRAN.R-project.org/package=DHARMa>.
- Heinen, J., Domínguez-García, V., Aguilera, G., Malsher, G., Vesterinen, E., Roslin, T., Bommarco, R., Bartomeus, I., 2024. Diversified cropping strengthens herbivore regulation by providing seasonal resource continuity to predators. *J. Appl. Ecol.* 1365-2664.14674 <https://doi.org/10.1111/1365-2664.14674>.
- Holland, J.M., Birkett, T., Southway, S., 2009. Contrasting the farm-scale spatio-temporal dynamics of boundary and field overwintering predatory beetles in arable crops. *BioControl* 54 (1), 19–33. <https://doi.org/10.1007/s10526-008-9152-2>.
- Holland, J.M., Reynolds, C.J.M., 2003. The impact of soil cultivation on arthropod (Coleoptera and Araneae) emergence on arable land. *Pedobiologia* 47 (2), 181–191. <https://doi.org/10.1078/0031-4056-00181>.
- Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S., Oaten, H., 2005. Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. *Spatiotemporal Dyn. Predat. beetles. JAE* 42 (6), 1140–1152. <https://doi.org/10.1111/j.1365-2664.2005.01083.x>.
- Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S., 2007. Spatio-temporal distribution and emergence of beetles in arable fields in relation to soil moisture. *Bull. Entom. Res.* 97 (1), 89–100. <https://doi.org/10.1017/S0007485307004804>.
- Jonsson, M., Kaartinen, R., Straub, C.S., 2017. Relationships between natural enemy diversity and biological control. *Curr. Opin. Insect Sci.* 20, 1–6. <https://doi.org/10.1016/j.cois.2017.01.001>.
- Knapp, M., Knappová, J., Jakubec, P., Vonička, P., Moravec, P., 2020. Incomplete species lists produced by pitfall trapping: how many carabid species and which functional traits are missing? *Biol. Conserv.* 245, 108545. <https://doi.org/10.1016/j.biocon.2020.108545>.
- Kober, K., Birkhofer, K., Glemnitz, M., 2024. High soil moisture promotes the emergence of ground beetles and spiders from soils in wheat fields. *BAAE* 80, 72–80. <https://doi.org/10.1016/j.baae.2024.09.001>.
- Lantmäteriet, 2018. Terrängkartan. Retrieved from: https://slu.primo.exlibrisgroup.com/discovery/openurl?institution=46SLUB_INST&vid=46SLUB_INST:SLUB_V1&url_ver=Z39.88-2004&rft.date=2018&rft_id=info:sid%2Fwiley&rft.genre=other&rft.title=Terr%EF%BF%BDbgkartan.
- Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G., Moreno, C.R., 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Syst.* 40 (1), 573–592. <https://doi.org/10.1146/annurev.ecolsys.110308.120320>.
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N.A., Carvalho, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandini, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardiñas, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tschamrtke, T., Vesely, M., Weisser, W.W., Wilson, J.K., Crowder, D.W.,

2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Change Biol.* 23 (11), 4946–4957. <https://doi.org/10.1111/gcb.13714>.
- Litovska, I., Van Der Plas, F., Kleijn, D., 2025. Arthropod abundance is most strongly driven by crop and semi-natural habitat type rather than management in an intensive agricultural landscape in the Netherlands. *AGEE* 378, 109298. <https://doi.org/10.1016/j.agee.2024.109298>.
- Luff, M.L., 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* 19, 345–357. <https://doi.org/10.1007/BF00348110>.
- Macfadyen, S., Hopkinson, J., Parry, H., Neave, M.J., Bianchi, F.J.J.A., Zalucki, M.P., Schellhorn, N.A., 2015. Early-season movement dynamics of phytophagous pest and natural enemies across a native vegetation-crop ecotone. *AGEE* 200, 110–118. <https://doi.org/10.1016/j.agee.2014.11.012>.
- Mesmin, X., Cortesero, A.M., Daniel, L., Plantegenest, M., Faloya, V., Le Ralec, A., 2020. Influence of soil tillage on natural regulation of the cabbage root fly *Delia radicum* in brassicaceous crops. *AGEE* 293, 106834. <https://doi.org/10.1016/j.agee.2020.106834>.
- Mestre, L., Schirmel, J., Hetz, J., Kolb, S., Pfister, S.C., Amato, M., Sutter, L., Jeanneret, P., Albrecht, M., Entling, M.H., 2018. Both woody and herbaceous semi-natural habitats are essential for spider overwintering in European farmland. *Agric. Ecosyst. Environ.* 267, 141–146. <https://doi.org/10.1016/j.agee.2018.08.018>.
- Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* 14, 20170213. <https://doi.org/10.1098/rsif.2017.0213>.
- Naturvårdsverket, 2018. Nationella marktäckedata 2018 basskikt, Sverige ver. 1.1. – <https://metadatakatalogen.naturvardsverket.se/metadatakatalogen/GetMetaDataById?id=8853721d-a466-4c01-afcc-9eae57b17b39>.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., Fitz John, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. *Vegan: Community Ecology Package*. R package version 2.6-4. (<https://CRAN.R-project.org/package=vegan>).
- Pfiffner, L., Luka, H., 2000. Overwintering of arthropods in soils of arable fields and adjacent semi-natural habitats. *AGEE* 78 (3), 215–222. [https://doi.org/10.1016/S0167-8809\(99\)00130-9](https://doi.org/10.1016/S0167-8809(99)00130-9).
- R core Team, 2023. R: a language and environment for statistical computing. R. Found. Stat. Comput. (<https://www.R-project.org/>).
- Ramsden, M.W., Menéndez, R., Leather, S.R., Wäckers, F., 2015. Optimizing field margins for biocontrol services: the relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. *AGEE* 199, 94–104. <https://doi.org/10.1016/j.agee.2014.08.024>.
- Rand, T.A., Tylanakis, J.M., Tschamtk, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9 (5), 603–614. <https://doi.org/10.1111/j.1461-0248.2006.00911.x>.
- Roger-Estrade, J., Anger, C., Bertrand, M., Richard, G., 2010. Tillage and soil ecology: partners for sustainable agriculture. *Soil Till. Res.* 111 (1), 33–40. <https://doi.org/10.1016/j.still.2010.08.010>.
- Roume, A., Ouin, A., Raison, L., Deconchat, M., 2011. Abundance and species richness of overwintering ground beetles (Coleoptera: Carabidae) are higher in the edge than in the centre of a woodlot. *Eur. J. Entomol.* 108, 615–622. <https://doi.org/10.14411/eje.2011.080>.
- Rowen, E.K., Regan, K.H., Barbercheck, M.E., Tooker, J.F., 2020. Is tillage beneficial or detrimental for insect and slug management? A meta-analysis. *AGEE* 294, 106849. <https://doi.org/10.1016/j.agee.2020.106849>.
- Sarthou, J.P., Badoz, A., Vaissière, B., Chevallier, A., Rusch, A., 2014. Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. *AGEE* 194, 17–28. <https://doi.org/10.1016/j.agee.2014.04.018>.
- Schneider, F.D., Brose, U., Rall, B.C., Guill, C., 2016. Animal diversity and ecosystem functioning in dynamic food webs. *Nat. Commun.* 7 (1), 12718. <https://doi.org/10.1038/ncomms12718>.
- Shannon, C.E., 1948. A mathematical theory of communication. *BSTJ* 27 (3), 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>.
- Shearin, A.F., Reberg-Horton, S.C., Gallandt, E.R., 2007. Direct effects of tillage on the activity density of ground beetle (coleoptera: carabidae) weed seed predators. *Environ. Entomol.* 36 (5), 1140–1146. [https://doi.org/10.1603/0046-225X\(2007\)36\[1140:DEOTOT\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2007)36[1140:DEOTOT]2.0.CO;2).
- Smith, R.G., Mortensen, D.A., 2017. A disturbance-based framework for understanding weed community assembly in agroecosystems: Challenges and opportunities for agroecological weed management. In: Wezel, A. (Ed.), *Agroecological Practices for Sustainable Agriculture*. World Scientific Publishing Europe, London, pp. 127–154. https://doi.org/10.1142/9781786343062_0005.
- Soane, B.D., Ball, B.C., Arvidsson, J., Basch, G., Moreno, F., Roger-Estrade, J., 2012. No-till in northern, western and south-western Europe: a review of problems and opportunities for crop production and the environment. *Soil Till. Res.* 118, 66–87. <https://doi.org/10.1016/j.still.2011.10.015>.
- Sutter, L., Amato, M., Jeanneret, P., Albrecht, M., 2018. Overwintering of pollen beetles and their predators in oilseed rape and semi-natural habitats. *AGEE* 265, 275–281. <https://doi.org/10.1016/j.agee.2018.06.030>.
- Tamburini, G., De Simone, S., Sigura, M., Boscutti, F., Marini, L., 2016. Conservation tillage mitigates the negative effect of landscape simplification on biological control. *JAEE* 53 (1), 233–241. <https://doi.org/10.1111/1365-2664.12544>.
- Thorbek, P., Bilde, T., 2004. Reduced numbers of generalist arthropod predators after crop management. *JAEE* 41 (3), 526–538. <https://doi.org/10.1111/j.0021-8901.2004.00913.x>.
- Tooker, J.F., O'Neal, M.E., Rodriguez-Saona, C., 2020. Balancing disturbance and conservation in agroecosystems to improve biological control. *Annu. Rev. Entomol.* 65 (1), 81–100. <https://doi.org/10.1146/annurev-ento-011019-025143>.
- Tortosa, A., Duflot, R., Rivers-Moore, J., Ladet, S., Esquerré, D., Vialatte, A., 2022. Natural enemies emerging in cereal fields in spring may contribute to biological control. *Agr. For. Entomol. Agric.* 24 (3), 267–278. <https://doi.org/10.1111/afe.12490>.
- Ullmann, K.S., Meisner, M.H., Williams, N.M., 2016. Impact of tillage on the crop pollinating, ground-nesting bee, *Peponapis pruinosa* in California. *AGEE* 232, 240–246. <https://doi.org/10.1016/j.agee.2016.08.002>.
- Welch, K.D., Harwood, J.D., 2014. Temporal dynamics of natural enemy-pest interactions in a changing environment. *Biol. Control* 75, 18–27. <https://doi.org/10.1016/j.biocontrol.2014.01.004>.
- Wilby, A., Thomas, M.B., 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecol. Lett.* 5 (3), 353–360. <https://doi.org/10.1046/j.1461-0248.2002.00331.x>.
- Zaller, J.G., Moser, D., Drapela, T., Frank, T., 2009. Ground-dwelling predators can affect within-field pest insect emergence in winter oilseed rape fields. *BioControl* 54 (2), 247–253. <https://doi.org/10.1007/s10526-008-9167-8>.