Combining organic fertilisation and perennial crops in the rotation enhances arthropod communities

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ABSTRACT

Single and combined diversification practices in crop fields and their effects on arthropod predators, decomposers and herbivores have mainly been assessed in small plot and cage experiments. In particular, effects of diversification on arthropod predators and their food resources, such as soil fauna, weed seeds and herbivorous prey in entire crop fields across the growing season, remain unclear. We explored how organic fertilisers, with or without the legacy of perennial ley in the crop rotation, and mineral fertiliser without the legacy of perennial ley, affected below- and aboveground communities in 19 spring cereal crop fields. In each field, we determined the abundance of the soil mesofauna, communities of arthropod prey aboveground and of the predator guilds carabids, staphylinids and spiders. We sampled at three crop stages: tillering, heading and ripening. Weed cover and soil characteristics, such as carbon and nitrogen content, were assessed. For most soil mesofauna groups, the combination of organic fertiliser with the legacy of ley gave highest, organic fertiliser with annual crop rotations intermediate, and mineral fertiliser with annual crop rotations the lowest total abundance. Aboveground arthropod prey abundances were similar across treatments. The legacy of ley increased richness of all aboveground arthropod predators. Staphylinid communities' abundance increased additively as diversification treatments were combined during tillering of the crop. Increasing organic amendments, alongside the reduced disturbances through inclusion of perennial ley in the rotation, led to more abundant communities below- and aboveground as well as more richness in aboveground predator communities.

1. Introduction

Intensive farming includes monoculture cropping systems dominated by high yielding crops in short rotations (Aguilar et al., 2015; Bennett et al., 2012) from which perennial grass-legume mixes and organic fertilisers often historically have been removed (Garrett et al., 2020; Martin et al., 2020; Naylor et al., 2005; Picasso et al., 2022) This has weakened the provisioning of ecosystem services such as biological pest regulation, soil fertility and nutrient cycling (Albizua et al., 2015; Dainese et al., 2019; Tamburini et al., 2020). (Re)-diversifying agriculture is suggested as a way to reverse these negative trends without penalising yields (Bommarco et al., 2013; Kremen and Merenlender, 2018; Kremen and Miles, 2012; Tittonell, 2014). Effects of single practices on single or few factors have been tested (Tamburini, 2020) but knowledge of outcomes of combined diversification practices on biodiversity and ecosystem functioning is still missing.

Crop field diversification practices include the use of organic amendments (Kremen and Miles, 2012; Tamburini et al., 2020) and perennial ley in crop rotations (Lemaire et al., 2015; Martin et al., 2020). Leys are mixes of perennial legume and grasses incorporated into crop rotations for feed production and fallow. Both practices enhance and maintain soil organic carbon pools (Scotti et al., 2015), which can promote local communities of beneficial organisms above- and belowground (Eyre et al., 2012; Marrec et al., 2015; Palmu et al., 2014; Tsiafouli et al., 2015). Short term plot experiments show that the diversification practice of adding organic fertilisers can support diverse and abundant communities of beneficial arthropods such as carabid beetles (Aguilera et al., 2020), but there are few examinations of combining this with other diversification practices (Tamburini et al., 2020). For instance, combining organic fertilisation and perennial leys in crop rotations, increases soil organic matter (SOM) and improves soil aggregation, providing complex habitats for soil fauna (Emmerling et al., 2021; Haynes, 1999). These effects could persist despite perturbations from annual cropping in subsequent years. Combined diversification might build abundances of below- and aboveground communities, which underpin ecosystem services such as pest regulation

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and nutrient cycling in crops following ley, but this remains to be tested for predators, herbivores and decomposers above- and belowground in arable fields and across the season.

Soil organisms in crop fields provide a number of ecosystem services that support crop production, such as decomposition, nutrient cycling and water regulation (Barrios, 2007; Kulmatiski et al., 2014). Soil food webs break down organic matter and release nutrients to the crops enhancing use efficiency of nutrients and reducing the need of mineral fertilisation (Bardgett and Chan, 1999). Organic fertilisers can increase soil diversity (Lin et al., 2019; Liu et al., 2016; Lori et al., 2017) and abundance of several taxa (Axelsen and Kristensen, 2000; Riggi and Bommarco, 2019). Benefits on abundance and diversity of soil organisms are, however, dependent of the quality of organic fertilisers applied (Viketoft et al., 2021). Perennial leys in crop rotations increase carbon and nitrogen content in the soil, improve its chemical and physical properties (Hoeffner et al., 2021) and benefit abundance and diversity of soil fauna communities (Crotty et al., 2016; Emmerling et al., 2021). Positive effects on abundance and diversity of soil organisms persist for several years after the transition from perennial leys to annual arable crops (Crotty et al., 2016). These legacy effects have been associated with lower disturbance of the soil with perennial crops (Lemaire et al., 2015) and increased habitat complexity through altered soil structure mediated by greater root development compared with annual crops (Marshall et al., 2016) and addition of SOM to the soil (Hernanz et al., 2009).

Organic fertilisers can enhance soil fauna abundance which constitutes a food resource for predatory arthropod communities above ground that contribute to the suppression and population regulation of crop herbivores (Birkhofer et al., 2008; Holland and Luff, 2000). Strengthened predator communities via increased availability of belowground prey has in short term plot experiments been seen to result in top-down suppression of aphid population abundance compared with mineral and no fertilisation (Aguilera et al., 2021; Riggi and Bommarco, 2019). The pest suppressive effect depends on fertiliser type and its quality to the soil fauna and herbivores (via impacts on plant quality) (Riggi and Bommarco, 2019). It remains unknown whether the top-down regulation effects are maintained across entire seasons and crop fields. Increasing alternative prey to predators via organic fertilisation could suppress pest populations by decoupling predator populations from dependence on only herbivores as prey. Prey communities generally fluctuate during the cropping season and if belowground prey is accessible already early in the season, this could stabilise aboveground predator communities at a time when herbivorous prey has not yet colonised the crop. The cascading effects of organic amendments on natural enemies' communities have to our knowledge not been quantified in multiple fields across the season.

To assess the effect of legacies of single and combined diversification practices on both soil mesofauna and aboveground arthropod predator and prey communities in arable fields, we compared three diversification practices: annual crop rotations receiving either mineral or organic fertilisers, and fields rotated with perennial ley receiving organic fertilisers. All farms in the region that had perennial ley in their crop rotation also applied organic fertiliser such that the combination of mineral fertilising and ley in rotation was not available. We sampled from early tillering of the crop until shortly before harvest to capture effects across crop development stages. We hypothesised that (1) adding organic fertilisers to a rotation with annual crops increases the abundance of soil mesofauna compared with fields receiving mineral fertiliser, (2) incorporating ley in the crop rotation further increases the soil fauna abundances, and (3) the abundance and diversity of aboveground arthropod predator communities increase as a result. We further expected, (4) no interactions among treatments and crop stages for soil mesofauna as they are locally bound to the fields, whereas (5) there is an interaction between treatment and crop stage for aboveground arthropod predator communities. The latter is due to aboveground predators colonising diversified fields at an earlier crop stage, as prey is already available in the form of soil fauna. During late crop stages, we expected aboveground arthropod predator communities to become more similar in abundance and diversity among treatments, as all fields provide a wider array of available prey to sustain aboveground predator communities.

2. Material and methods

2.1. Study area and site selection

We selected 19 conventionally managed fields with spring-sown cereals (oats and barley) located in Halland county along the SW coast of Sweden (56.85° N, 12.85° E). The county is dominated by agricultural crop and animal production with high productivity due to ample annual rainfall of 700–800 mm and long days in the growing season. Sampling of above- and belowground arthropod communities was carried out during three crop stages in 2020, at tillering (early May, approx. 20 days after sowing), during heading (early June) and during early ripening (early July). Crop stages were assessed according to Large (1954). Prior to our experiment, fields differed in their crop rotation (see additional information on crop rotations in Table A.1) and received either mineral or organic fertilisation. Treatments included fields that only received mineral fertiliser and were rotated with annual crops (FminRa; n = 6), fields treated with organic fertilisers (manure and slurry, see Table A.2) rotated with annual crops (ForgRa; n = 7) and fields treated with organic fertiliser where crop rotation included 3 years of perennial leys (ForgRl, n = 6). All farms in this region with perennial leys in their crop rotation applied organic fertilisers, such that the design could not be fully crossed. The fields were managed under the respective treatment for a minimum of six years. At sampling, fields rotated with ley had been without ley for at least two years. We thereby captured legacy effects instead of immediate pre-crop effects. All fields were ploughed regularly. Crops were sown between 7th and 15th of April 2020. To control for comparable conditions for soil mesofauna sampling, soil texture was assessed based on farmer's knowledge of their field and balanced across treatments. Soil textures were later formally confirmed using the soil composite samples for soil content analysis (see additional information Table A.1 and Section 2.6). Crop rotation information was obtained through farmer questionnaires and the Integrated Administration and Control System (IACS), administered by the Swedish board of Agriculture.

To verify that treatments were not affected by the surrounding landscape composition, we calculated the percent of arable land and forest in a 500 m radius around each study site as both represented dominant habitat types in this region. Calculations were based on digital land cover maps (Terrängkartan, Lantmäteriet, 2018, IACS). We found that the proportions of the landscape characteristics were balanced across treatments (Table A.1).

2.2. Experimental set up

In each field, we set up a sampling area of 25 × 50 m after sowing in which no insecticides were applied in agreement with the farmers. Herbicides and fungicides were applied in the sampling area same as in the rest of the field according to each farmers individual decision. The sampling areas were placed either at the field border or inside the field depending on farmer's need and soil type. The placement of the sampling area at the border or inside the fields was balanced across treatments (see Table A.1). Sampling took place along two 30 m long transects with four sampling points in each. To avoid the effect of insecticide spray drift, transects were placed at 8 and 14 m from the border of the sampling area (Figure A.1). The same sampling effort was applied in all fields allowing for relative comparisons of communities among fields.

2.3. Soil mesofauna community sampling

Soil mesofauna was sampled by taking four intact soil cores (5 cm diameter and 10 cm depth) per field at all three crop stages. Soil core sampling with subsequent extraction is a widely used method for estimating soil mesofauna occurrences (e.g., González et al., 2021) robust to biases from other techniques that often fail to capture less mobile species. Soil cores were taken at two sampling points per transect and refrigerated at 4 °C until Tullgren extraction (Tullgren, 1918). The extraction lasted for four days with a gradual increase over the first 24 h to a target temperature of 52 °C that was held constant for the remaining 72 h. All collected soil mesofauna was preserved in a glycol-ethanol solution (80 % ethanol) until sorting in the lab. Individuals were counted and assigned to the following five groups: Collembola, Mesostigmata, Oribatida, juvenile Acari, and other arthropods (individuals >2 mm, e.g., millipedes).

2.4. Aboveground arthropod predator community sampling

In each transect, we placed four pitfall traps, approximately 3.5 m apart, resulting in eight pitfalls per field. Plastic cups (12 cm diameter, 12 cm deep) were placed into the soil and filled with approximately 200 ml of water with added odourless detergent. During each crop stage sampling, pitfall traps remained open for four consecutive days. Operating pitfalls over a set period allows adequate assessment of mobile predators, as they capture a large number of invertebrates, removing biases in abundances of rare specimens arising from one-time snapshot sampling. Collected specimen were stored in 70% ethanol and identified in the lab. All spiders and carabid beetles were identified to species, staphylinid beetles to genus.

2.5. Aboveground arthropod prey community sampling

Aboveground arthropod prey communities were sampled during mid and late crop stage when the crop had grown enough for herbivores to establish in the crop and allowing for sampling them with sweep nets, which was not possible in the early crop stage. Sweep netting hereby samples organisms dwelling on the crop or flying within the crop canopy allowing adequate assessment of the relative amount of available prey for predators. Two corridors for sweep netting were established in 1 m distance to the pitfall track transect to avoid interference with the pitfall traps. Along the two sweep netting transects, four sweeps with 15 strikes each were taken. Caught insects were transferred into plastic bags and stored in the freezer before storing them in 70 %-ethanol up until identification.

Individuals were counted and compiled within the following three groups: flies, small herbivores and large herbivores. Flies included Diptera belonging to the suborder or families Syrphidae, Chloropidae, Brachycera and Nematocera. Small herbivores (<2 mm) included Aeolothripidae, other Thysanoptera and Aphidoidea. Large herbivores included Apionidae, Curculionidae and Miridae.

2.6. Soil content sampling

We took five soil cores (5 cm diameter, 10 cm depth) and pooled them into one composite sample per field. Sampling took place once during early crop stages. Samples were analysed for soil organic matter (SOM), total nitrogen and total carbon contents (https://www.agrilab.se).

To assess soil moisture, eight soil core samples (2.5 cm diameter, 10 cm depth) were taken during each sampling round in early, mid and late crop stage near each pitfall trap. Samples were weighed before and after drying in the oven at 80 °C for 24 h. Soil moisture was assessed as the percentage difference in weight.

2.7. Community metrics

To characterise community differences among treatments, we calculated the abundance caught separately for each of the five soil mesofauna groups, the three aboveground arthropod prey groups as well as activity density of predators from the pitfall traps (hereafter: total abundance). Total abundance was defined as the number of captured individuals per field and crop stage by summing up the number of individuals caught in each replicate sample separately for each organism group. Therefore, total abundance is relative to the sampling method but comparable between treatments. Non-transformed total abundance of soil mesofauna was used in all analysis. For the visual presentation in Fig. 1, soil fauna abundances were re-scaled to the unit of individuals per m² in order to simplify comparability with other studies that most often present results from this sampling method in that unit.

Predator richness and Shannon diversity were calculated separately for the three predator groups of carabids, staphylinids and spiders. Predator richness was defined as the number of recorded species (carabids and spiders) or the number of recorded genus (staphylinids) per field and crop stage summed across replicate samples within each field and calculated separately for each organism group. Shannon diversity was calculated using the Shannon-Wiener index, where pi describes the proportion of the entire community made up of species i.

$$H = -\Sigma pi * \ln(pi)$$

All calculations were made within the "vegan" package (Oksanen et al., 2020).

## 2.8. Statistical analysis

2.8.1. Species communities

Generalised linear mixed models were used to assess the effect of diversification treatments (FminRa, ForgRa and ForgRl) and crop stage on the community metrics: i.e., total abundance for the five soil mesofauna groups and three aboveground arthropod prey groups as well as total abundance, predator richness and Shannon diversity for carabids, staphylinids and spiders. Individual models were fitted for each community metric and predator group. Each model included the interaction between diversification treatment and crop stage as fixed factors and field identity as random factor. We first built full models and then simplified them by removing non-significant (p > 0.05) interaction terms. We always kept the single terms, as they were part of the experimental design. Models on soil mesofauna abundances were fitted using non-scaled data referring to the non-transformed total abundance per field and crop stage. To achieve optimal model fit for small herbivores, we had to further simplify the model by dropping the random effect of field identity. To test the effect of sampling areas being located at the border or the inside the field, we included sampling area location as a random effect crossed with field identity. However, sampling area location did not explain any further variation and was therefore excluded.

Normal- or negative binomial distribution were used, depending on the distribution of residuals in each analysis. Error distributions were chosen to obtain optimal model fit (see 2.8.3 Model assumptions and fit) with negative binomial distribution for all mesofauna, aboveground arthropod prey and aboveground arthropod predator total abundance models and normal distribution for aboveground arthropod predator predator richness and Shannon diversity.

2.8.2. Soil quality analysis

Linear models were used to assess the effect of diversification treatments on the soil metrics.

soil organic matter, total nitrogen and total carbon contents, with treatment as a fixed factor. Individual models were fitted for each of the soil metrics. The effect of treatments on soil moisture was tested using a generalised linear mixed model. The interaction between diversification
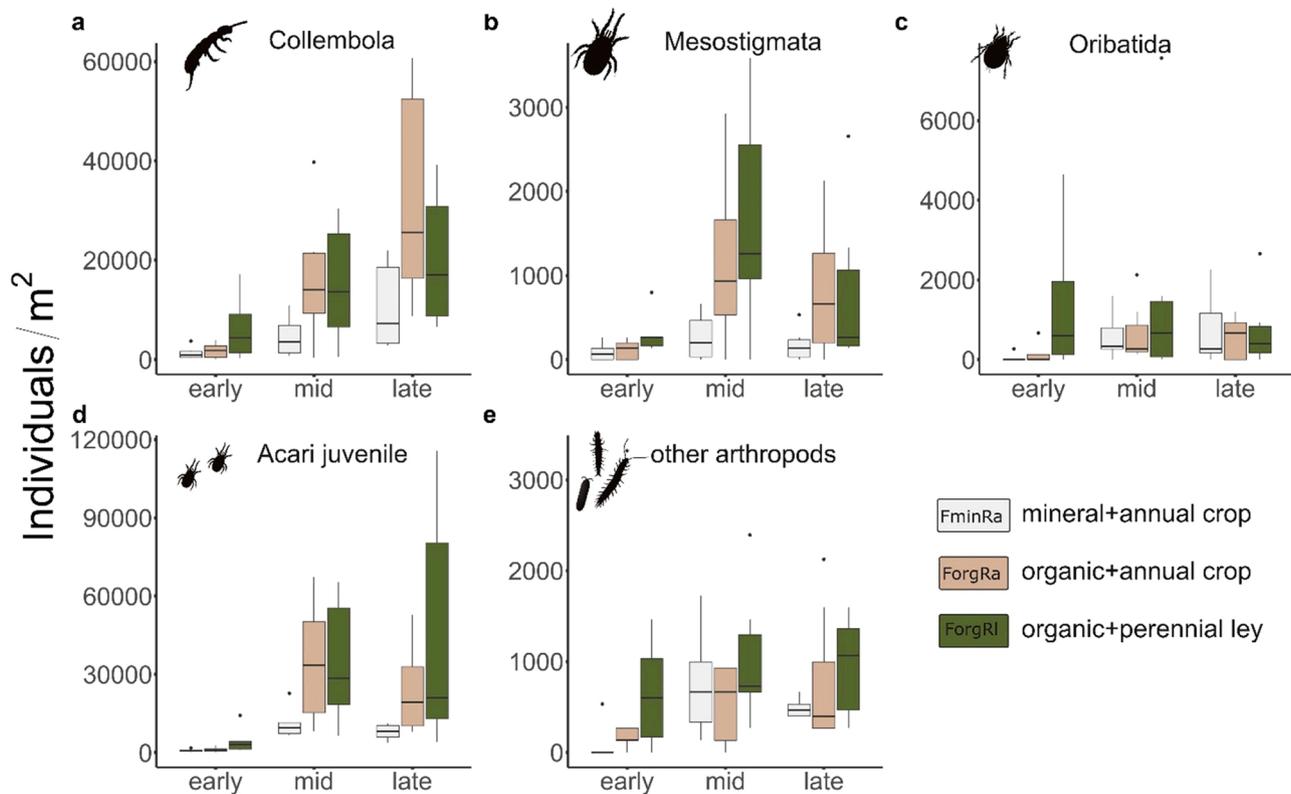
Fig. 1. Total abundances expressed as the number of individuals per m^2 of the five soil mesofauna groups: Collembola (a), Mesostigmata (b), Oribatida (c), juvenile Acari (d) and other arthropods (e) for three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green) during early, mid and late crop stage.

treatment and crop stage was included as fixed factors and field identity as random factor. Normal distribution was chosen based on residuals of the model.

2.8.3. Model assumptions and fit

We checked and validated model assumptions and fit by testing for over- and underdispersion and visually inspecting residual diagnostics of scaled residuals simulated from the model fit, i.e., deviation from uniformity and observed against predicted residuals. We calculated conditional and marginal R^2 (Nakagawa et al., 2017) implemented in the "performance" package (Lüdecke et al., 2021). Parameter significance was tested using Type II-Wald chi-square tests. Estimated marginal means were obtained using a Tukey post-hoc test within the "emmeans" package version 1.7.2 (Russell and Lenth, 2022).

All data were analysed using R version 4.1.1 (R Core Team, 2020) and packages "glmmTMB" version 1.1.2.9000 (Brooks et al., 2017),

"stats" version 4.1.1, "DHARMa" version 0.4.5 (Hartig, 2021), "car" version 3.0–12 (Fox and Weisberg, 2019).

3. Results

In total, we sampled 14,048 individuals of soil mesofauna, 17,787 aboveground arthropod predators and 13,330 individuals of aboveground arthropod prey. Collembola and juvenile Acari were the most abundant groups of soil mesofauna (37 %, 55 % respectively) followed by Oribatida (2 %), Mesostigmata (1.8 %) and other arthropods (2.2 %). Carabids and staphylinids were the most abundant predator groups making up 34 % and 41 % of all predators respectively, followed by spiders making up 25 % of all sampled predators. Aboveground arthropod prey were dominated by small herbivores (mainly Thysanoptera) with 78 % followed by flies with 20 % and large herbivores with 2 % of the overall community. Table 1.

Table 1
Test statistics with χ^2-value, degrees of freedom, p-value, marginal and conditional R^2 for each model test on the effects of treatment and crop stage on total abundance of the five soil mesofauna groups. Statistically significant (p < 0.05) results are in bold, trends in italic (0.05 <p > 0.1). Test statistics including pairwise comparisons of treatments reporting their estimates, standard errors (SE), t-ratio and p-values can be found in supplementary Tables A.5.1 and A.5.2.

	Response variable	Explanatory variable	χ^2	DF	p-value	R^2_m	R^2_c
Collembola	Total abundance	Treatment	5.948	2	*0.051*	0.575	0.886
		Crop stage	141.829	2	**< 0.005**		
		Treatment: crop stage	14.727	4	**0.005**		
Mesostigmata	Total abundance	Treatment	8.961	2	**0.009**	0.496	0.778
		Crop stage	34.333	2	**< 0.005**		
Oribatida	Total abundance	Treatment	2.187	2	0.335	0.391	0.698
		Crop stage	5.186	2	*0.074*		
		Treatment* crop stage	9.310	4	*0.053*		
Acari juvenile	Total abundance	Treatment	14.594	2	**< 0.005**	0.772	0.887
		Crop stage	207.949	2	**< 0.005**		
Other arthropods	Total abundance	Treatment	4.016	2	0.134	0.242	0.403
		Crop stage	7.267	2	0.026		

3.1. Soil mesofauna

Collembola, Oribatida and juvenile Acari were most abundant in fields with organic fertilisation and perennial leys (ForgRl), intermediately abundant in fields receiving organic fertiliser and annual crops (ForgRa) and fewest in fields receiving mineral fertiliser and annual crops in the rotation (FminRa; Table A.5.1, Table A.5.2, Fig. 1). Treatment effects on Collembola and Oribatida abundances were dependent on the crop stage (Table1) with additive effects of treatments found at both early and mid-crop stage for Collembola (Table A.5.2) and at early crop stage for Oribatida (Table A.5.2). The total abundance of Mesostigmata was enhanced in fields receiving organic fertiliser combined with ley compared with fields receiving mineral fertiliser combined with annual crop rotations (Fig. 1, Table A.5.1). The abundance of other arthropods was not affected by treatment but increased from early to mid-season (Fig. 1, Table A.5.1).

3.2. Aboveground arthropod prey

We found no difference in aboveground arthropod prey abundances among the diversification treatments for flies (Figure A.4.1, Table A.4), small herbivores (Figure A.4.1, Table A.4) and large herbivores (Figure A.4.1, Table A.4).

3.3. Aboveground arthropod predators

3.3.1. Total abundance

Total abundance of carabid beetles was only marginally affected by the treatments (Table 2) with lower abundances in ForgRa fields compared with both FminRa and ForgRl (Table A.5.1, Fig. 2). Carabid total abundances increased with the succession of crop stages (Table A.5.1, Fig. 2). The total abundance of staphylinids was explained by the interaction of treatment and crop stage (Table 2) with highest staphylinid abundances in ForgRl, intermediate abundances in ForgRa and lowest in fields with FminRa (Table A.5.2, Fig. 2) only during early crop season. The total abundance of spiders was explained by the interaction of treatment and crop stage (Table 2, Fig. 2). *Post hoc* comparisons showed higher abundances in FminRa and ForgRl than in ForgRa (Table A.5.2) in late crop stage.

3.3.2. Predator richness

Carabid species richness was explained by treatment and crop stage (Table 2, Fig. 2) with higher species richness in ForgRl fields compared to ForgRa (Table A.5.1) and marginally higher species richness in ForgRl compared with FminRa (Table A.5.1). Carabid species richness increased from early to late (Table A.5.1) crop stage. The genus richness of Staphylinids was explained by treatment and crop stage (Table 2, Fig. 2) with higher genus richness in ForgRl fields than in FminRa fields (Table A.5.1). Staphylinid genus richness gradually increased from early to late crop stage (Table A.5.1).

The species richness of spiders was explained by the interaction of treatment and crop stage (Table 2, Fig. 2) with increased species richness in ForgRl than in FminRa in early season (Table A.5.2).

3.3.3. Shannon diversity

There were no treatment differences for Shannon diversity of carabid communities, but Shannon diversity increased from mid to late crop stage (Table 2, Fig. 2, Table A.5.1). Shannon diversity of staphylinid communities was explained by both treatment and crop stage (Table 2, Fig. 2) with marginally increased Shannon diversity in ForgRl fields compared to ForgRa fields (Table A.5.1) and increased Shannon diversity in mid compared to both early and late crop stage (Table A.5.1). Shannon diversity of spider communities was explained by the interaction of treatment and crop stage (Table 2, Fig. 2). During early season, spider Shannon diversity was marginally enhanced in ForgRl compared with FminRa (Table A.5.2). The reverse effect was found in mid-crop stage with lower Shannon diversity in ForgRl fields compared with ForgRa and FminRa (Table A.5.2).

3.4. Soil quality

Soil organic matter (SOM), nitrogen as well as carbon content were explained by treatments (Table 3) and enhanced only under the combined diversification of organic fertiliser and perennial ley in crop rotation (Table A.2.1, Figure A.2.1). The difference in soil moisture was explained by the interaction of treatment and crop stage (Table 3). Fields under combined diversification with organic fertiliser and perennial ley in the crop rotation had higher soil moisture compared to both, fields with mineral fertiliser and annual crop rotations and fields with single diversification of organic fertiliser and annual crop rotation, during
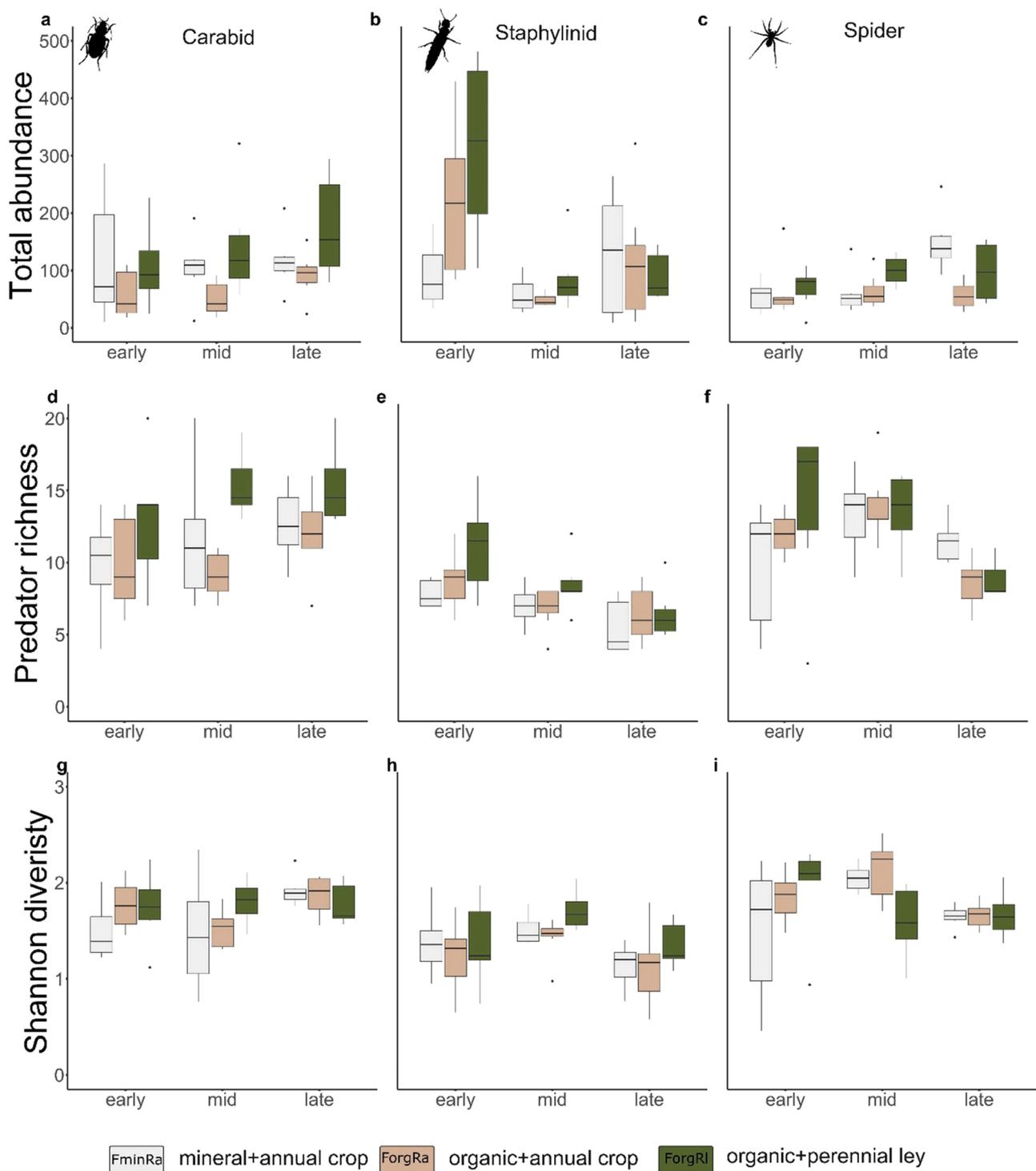
Table 2

Test statistics with χ^2-value, degrees of freedom, p-value, marginal and conditional R^2 for each model tests on the effects of treatment and crop stage on the respective community response variables for the three predator groups. Statistically significant ($p < 0.05$) results are in bold, trends in italic ($0.05 < p > 0.1$). Test statistics including pairwise comparisons of treatments reporting their estimates, standard errors (SE), t-ratio and p-values can be found in supplementary Tables A.5.1 and A.5.2.

	Response variable	Explanatory variable	χ^2	DF	p-value	R^2_m	R^2_c
Carabids	Total abundance	Treatment	5.857	2	*0.053*	0.246	0.649
		Crop stage	9.974	2	**0.006**		
	Species richness	Treatment	10.613	2	**0.004**	0.308	0.589
		Crop stage	9.667	2	**0.007**		
	Shannon diversity	Treatment	2.098	2	0.350	0.149	0.149
		Crop stage	7.738	2	**0.020**		
Staphylinids	Total abundance	Treatment	3.614	2	0.164	0.466	0.539
		Crop stage	30.210	2	**< 0.005**		
		Treatment* crop stage	11.709	4	**0.019**		
	Genus richness	Treatment	7.236	2	**0.026**	0.388	0.515
		Crop stage	31.870	2	**< 0.005**		
	Shannon diversity	Treatment	4.735	2	*0.093*	0.262	0.332
		Crop stage	15.762	2	**< 0.005**		
Spiders	Total abundance	Treatment	4.996	2	*0.082*	0.351	0.533
		Crop stage	10.062	2	**< 0.005**		
		Treatment* crop stage	17.912	4	**0.001**		
	Species richness	Treatment	0.342	2	0.842	0.352	0.507
		Crop stage	25.919	2	**< 0.005**		
		Treatment* crop stage	13.532	4	**0.008**		
	Shannon diversity	Treatment	1.998	2	0.368	0.288	0.390
		Crop stage	7.870	2	**0.019**		
		Treatment* crop stage	15.640	4	**0.003**		

Fig. 2. Total abundance expressed as individuals caught per field using eight pitfall traps (a-c), predator richness (d&f=species richness; e=genus richness) and Shannon diversity (g-i) for the three natural enemy guilds carabids, staphylinids and spiders for the three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green) during early, mid and late crop stage.

early and mid-crop stage (Figure A.2.2, Table A.2.2).

4. Discussion

The combined effect of organic fertilisation and legacy of ley enhanced abundance of soil mesofauna and affected abundance, predator richness and Shannon diversity of some, but not all, aboveground arthropod predators. Community differences across treatments occurred mostly in the early- and mid-crop stages. In contrast to our expectations, we found no differences among treatments for the abundance of aboveground arthropod prey at any crop stage. Combining organic fertilisation and perennial ley in the crop rotation consistently enhanced SOM, nitrogen and carbon content and moisture in the soil.

Table 3

Test statistics with sum of squares (lm) or χ^2-value (glmm), degrees of freedom, p-value, marginal (lm, glmm) and conditional R^2 (glmm) for each model tests on the effects of treatment and crop stage on the respective community response variables soil organic matter (SOM), nitrogen- and carbon content as well as soil moisture of agricultural soils. Statistically significant (p < 0.05) results are in bold, trends in italic (0.05 <p > 0.1). Test statistics including pairwise comparisons of treatments reporting their estimates, standard errors (SE), t-ratio and p-values can be found in supplementary Table A.2.1.

	Metric	Explanatory variable	Sum of squares / χ^2	DF	p-value	R^2_m/R^2_c
Lm	SOM	Treatment	39.432	2	**0.002**	0.525/-
	Nitrogen content	Treatment	3.315	2	**0.008**	0.450/-
	Carbon content	Treatment	1075.0	2	**0.005**	0.482/-
Glmm		Treatment	8.348	2	**0.0153**	
	Soil moisture	Crop stage	287.819	2	**< 0.005**	0.48/0.952
		Treatment*crop stage	23.550	4	**< 0.005**	

4.1. Diversification effect on abundances of soil mesofauna

As expected, diversification increased the total abundance of soil mesofauna compared with annual crop rotation with mineral fertiliser (Viketoft et al., 2021). The highest abundances occurred when organic fertilisers and perennial ley in the crop rotation were combined. Only marginally statistically significant effects were apparent for some groups (e.g., Collembola) and for the single effect of organic fertiliser, but trends in effect sizes were consistent for all soil fauna groups.

Strong effects on soil mesofauna under combined diversification were expected as soil mesofauna depend not only on food resources, but also other niche dimensions such as disturbance and habitat quality (Coulibaly et al., 2022; Purvis and Curry, 1980). Long term fertilisation plot experiments showed variable effect of organic fertiliser on soil mesofauna abundances depending on fertiliser type and quality (Aguilera et al., 2021; Viketoft et al., 2021). Interestingly, our field study showed that soil mesofauna consistently benefited from the addition of organic fertiliser alone despite differences in fertiliser type among fields and low replication of study sites. Addition of organic fertiliser improves conditions for the mesofauna, most probably by increasing their food resources both in the form of organic matter but more importantly by increasing the microorganisms that colonise organic matter (Potapov et al., 2022). To assess the impact of diversification on microorganisms, soil microbial quality indicators such as total microbial biomass (C_{mic}) need to be measured which was not done in the present study. However, SOM was measured which gives an indication of microbial biomass C_{mic} constituting food resources for most microorganisms (Gentry and Zuberer, 2021). We therefore speculate that high amount of SOM under combined organic fertilisation and perennial crops likely resulted in higher mesofauna abundance.

We found that perennial leys in the crop rotation combined with organic fertilisers increased soil moisture (Figure A.2.2), potentially creating favourable habitat and microclimatic conditions for soil mesofauna (Franzluebbers et al., 2014; Yazdanpanah et al., 2013). Especially soft bodied organisms, such as Collembola and juvenile Oribatida and Mesostigmata, are prone to desiccation and dependent on sufficient soil moisture for reproduction and growth (Tsiafouli et al., 2005; Wang et al., 2022). Additionally, the lower disturbance associated with perennial leys in the rotation could contribute to enhancing soil mesofauna communities overall. Given that our fields had been without ley for two years prior to sampling suggests that such positive effects on soil mesofauna communities can persist for several years after the ley has been removed (Crotty et al., 2016). Farming practices that provide food and habitat for beneficial organisms show promise to enhance ecosystem services, such as decomposition, nutrient cycling and crop protection mediated by soil mesofauna.

4.2. Diversification effects on predators and prey

Despite consistent positive effects on soil mesofauna communities, treatment effects did not directly propagate to all aboveground predator groups. Staphylinid communities showed the hypothesised stepwise increase in abundances, with highest abundances under combined diversification with organic fertiliser and perennial ley, intermediate abundances under single diversification with organic fertiliser and lowest abundances in fields with mineral fertiliser, during early season. Predator richness was highest under combined diversification with organic fertilisers and perennial ley. Treatment effects on spider communities differed across crop stages with highest species richness during tillering of the crop in fields under combined organic fertiliser and perennial ley, but highest abundances in late crop session in fields receiving mineral fertiliser.

Various food resources are available in crop fields. We found abundances of aboveground herbivore and Diptera prey to be similar across treatments (Figure A.4) but alternative food resources differed among treatments. Fields with mineral fertilisers had higher weed cover, which could provide alternative food resources such as weed seeds, whereas fields with combined organic fertiliser and leys harboured higher soil fauna abundances (Fig. 1). Predators may be able to exploit these resources, which would explain the weak differences of carabid predator abundances between fields with mineral fertiliser in comparison to organic fertiliser in combination with perennial ley that we observed. This might affect the regulation of the herbivore populations positively if more generalist predators are sustained in the field or negatively if the predator community becomes dominated by other specialists, such as weed seedeaters that do not feed on herbivores.

Several species of arthropod predators are known to overwinter in agricultural soils and community build-up is negatively affected by cropping practices that disturb the soil and deplete soil organic carbon (Hanson et al., 2016; Holland et al., 2009). Positive effects of diversified practices, mainly through the inclusion of perennial leys, on staphylinid abundances occurring during early season, suggest that local build-up of communities could be facilitated by improved reproduction and overwintering success with reduced disturbance in the field (Martin et al., 2020). Comparisons between spring emergence in ley and cereal crop fields, showed lower dispersal tendency of staphylinids in ley fields suggesting that staphylinids tend to disperse less in undisturbed habitats (Hanson et al., 2016). Thus, build-up and high concentration of natural enemies in the field during early season would give the predators a head start to predate on later arriving pests (Costamagna et al., 2015; Settle et al., 1996). Simultaneous assessment of emergent and colonising communities of predators could further elucidate the link between pest control and predator community build- up within fields under agricultural diversification.

Additionally, the reduced disturbance supports species rich and diverse arthropod communities (Tamburini et al., 2016; Tooker et al., 2020), explaining the positive effects of diversification with perennial leys in combination with organic fertiliser on predator richness of all groups in our study. In addition, other habitat dimensions such as soil moisture were highest under combined organic fertilisation and inclusion of perennial leys in the crop rotation (Figure A.2.2) potentially contributing to enhanced overwintering success. Sustaining abundant and rich communities increases community resilience under continuous disturbance from cropping. More diverse predator communities exploit a greater variety of resources (Byrnes et al., 2014), and biodiversity associated to agroecosystems can aid ecosystem functioning such as

biological weed and pest control (Soliveres et al., 2016), allowing the coexistence of abundant service providing aboveground predator communities.

Further, disturbance from cropping practices is understood to reduce diversity of soil food webs and results in communities consisting of smaller bodied organisms (Tsiafouli et al., 2015). This could have implications for bottom-up regulation of aboveground predators by soil mesofauna, whereby smaller bodied prey do not provide enough food resources to sustain aboveground predator populations. We did not test for differences in body size in the soil fauna communities, but suggest that the belowground food web probably benefits from lower disturbance and organic subsidies which is likely to strengthen top- down regulation of herbivores (Zelnik et al., 2022).

4.3. Conclusion

We investigated the effect of combined diversification on arthropod communities below and aboveground in crop fields. We conclude that adding organic materials in combination with perennial ley in the crop rotation enhances soil mesofauna abundances and subsequently benefits aboveground predators, in particular staphylinids. While highly abundant soil mesofauna could have sustained predator communities in diversified fields, high weed seed availability could have sustained predators in non-diversified fields leading to less clear differences in predator communities as expected. However, our results highlight that careful assessment of different available prey in the fields is crucial in understanding predator responses to management practices. A more highly replicated study to ascertain statistically significant effect differences, in which feeding links in the food web are also explicitly assessed, e.g., via molecular gut content analysis (e.g. Krey et al., 2021; Roubinet et al., 2017), would clarify these relations.

Lower disturbance in highly diversified fields through extended crop rotations with perennial ley, could have benefits for the overwintering success of predators. It is, hence, possible that pest suppression in fields with low diversification are more dependent on attracting predators from the surrounding landscape. Adopting cropping practices that combine organic fertilisation with extended crop rotations that include perennial leys holds potential to foster biodiversity and increase resilience of communities and ecosystem functions below- and aboveground.

CRediT authorship contribution statement

J.H, M.E.S, R.B conceived the ideas. J.H, M.E.S, R.B, A.T designed the methodology; J.H and M.E.S collected the data; J.H analysed the data and led the writing of the manuscript. R.B & M.E.S supervised the manuscript preparation. All authors contributed to the drafts and gave approval of the final manuscript.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108461.

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