



Effects of field-level strip and mixed cropping on aerial arthropod and arable flora communities

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ABSTRACT

Loss of arthropod biodiversity can impair the provision of ecosystem services in agricultural landscapes. Crop diversification strategies offer the possibility to support arthropod communities without putting aside agricultural land as conservation areas. Within-field crop diversification measures, such as strip cropping and crop mixtures, may provide arthropods with continuity and diversity in food, shelter and habitat at fine spatial and temporal resolutions. However, it is unclear how strip cropping and plant species diversity within strips influences aerial arthropod and weed communities in commercially sized arable fields. In this 2-year study we tested the effects of crop heterogeneity on aerial arthropod and plant communities in organically managed strip fields. We tested effects of configurational crop heterogeneity by comparing sole cropping (*MONO*) with strip cropping (*STRIP*), and compositional crop heterogeneity by comparing *STRIP* with flower-legume-grain crop mixtures grown in strips (*STRIPMIX*). Aerial arthropod communities were assessed in 138 sweep net transects and plant communities in 124 vegetation plots in cabbage, wheat, sugar beet and barley. Higher configurational crop heterogeneity by strip cropping reduced herbivore abundances and increased natural enemy species richness in organic cabbage strips. Cabbage in *MONO* had a significantly higher herbivore abundance (+11%) and a lower natural enemy species richness (−57%) than cabbage in *STRIP*. Higher compositional crop heterogeneity by sowing additional plant species in strips (*STRIPMIX*) significantly increased plant abundance (+33%), plant species richness (+21%), total aerial arthropod abundance (+45%), and total aerial arthropod species richness (+21%) compared to *STRIP*. Our work shows that both configuration of crop areas (*MONO* vs. *STRIP*) and plant species diversity within strips (*STRIP* vs. *STRIPMIX*) can support arthropod biodiversity and natural pest suppression, but that arthropod responses differ between diversification strategies and crop combinations. Further optimization of design and management of within-field crop diversification strategies holds potential to attain biodiversity-based cropping systems which deliver multiple ecosystem services and have a reduced dependency on pesticides.

1. Introduction

The widespread decline of arthropod populations has raised public awareness and concern about a potentially imminent biodiversity crisis (Shortall et al., 2009; Hallmann et al., 2017; Goulson, 2019; Wagner et al., 2021). Loss of arthropod biomass and species richness pose serious threats to ecosystem functioning as arthropods deliver multiple ecosystem services, such as pollination and pest suppression (Dainese

et al., 2019). Furthermore, arthropods are a key component of terrestrial food-webs and loss of arthropod communities have cascading impacts on higher taxa such as mammals and birds (Hallmann et al., 2014; Wagner et al., 2021). While multiple drivers appear responsible for the widespread arthropod decline, agricultural intensification has been pointed out as a key-stressor (Habel et al., 2019; Sánchez-Bayo and Wyckhuys, 2019; Raven and Wagner, 2021; Wagner et al., 2021). Intensified agricultural cropping landscapes are characterized by large

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homogeneously managed areas planted with a single genotype (van der Zanden et al., 2016), and field sizes that have increased over the past decades (Clough et al., 2020). Field enlargement in combination with a decrease in the diversity of crop species, varieties and genotypes have contributed to an ongoing homogenization of agricultural landscapes (Baessler and Klotz, 2006; Baguette and Van Dyck, 2007; Rodríguez and Wiegand, 2009; Clough et al., 2020; Khoury et al., 2022). Such simplified, homogeneous and coarse-grained landscapes provide a limited diversity and continuity of food resources, shelter and habitat, which can make these landscapes difficult environments for a wide range of arthropod taxa (Fahrig et al., 2015; Haan et al., 2021).

Growing evidence suggests that fine-grain landscapes with high crop heterogeneity can play a major role in supporting farmland biodiversity (Benton et al., 2003; Sirami et al., 2019), including arthropod diversity (Bertrand et al., 2016). Crop heterogeneity is composed of configurational heterogeneity (e.g. field size) and compositional heterogeneity (e.g. plant species diversity) (Sirami et al., 2019). While increasing configurational heterogeneity in agricultural landscapes by reducing mean field sizes runs counter to the current trend of increasing scale enlargement (Clough et al., 2020), it has high potential for supporting farmland arthropod communities (Fahrig et al., 2011; Lichtenberg et al., 2017; Martin et al., 2019). One way of reducing mean field sizes is the practice of growing different crops side by side in strips that can differ in width and length, so-called strip cropping. The practice of growing crops in strips allows independent crop management per strip with standard farm machinery, but supports ecological interactions between strips by mimicking a diverse crop mosaic at a small scale (Ditzler et al., 2021).

Whilst studies on the influence of crop diversity on arthropod communities have a long history (Pimentel, 1961; Altieri et al., 1984; Andow, 1991), the effects of field size (configurational heterogeneity) on arthropod communities have only recently been addressed (Sirami et al., 2019). There is generally broad support that decreasing field size increases arthropod abundance and species richness, and that this positive effect is mediated by a combination of more non-crop area and increased edge density from crop/crop edges (Lichtenberg et al., 2017). Findings of strip crop experiments provide partial support for the positive effect of edge density on arthropod communities (Ditzler et al., 2021; Alarcón-Segura et al., 2022). Ditzler et al. (2021) found significantly higher spider, rove beetle, harvestmen and non-*Pterostichus* carabid activity densities and species richness in organic strip cropped wheat fields (3 or 6 m), compared to monoculture wheat fields using pitfall traps. Alarcón-Segura et al. (2022) found higher spider activity density and richness in conventional strip cropped oilseed rape and wheat fields (27 or 36 m) than in monoculture oilseed rape. On the other hand, beetle activity density and richness was lower in winter wheat and oilseed rape strips than in monoculture oilseed rape (Alarcón-Segura et al., 2022). Both studies provide valuable evidence of the biodiversity benefits of strip cropping wheat and oilseed rape. However, it remains unknown how more mobile aerial arthropod communities respond to strip cropping configurations with different crops. Furthermore, it is still unclear how aerial arthropod communities respond to further diversification in strip cropping systems which contain multiple plant species within the strip.

This 2-year study aimed to elucidate how field-level diversification through strip cropping single crop species and crop mixtures affected plant and aerial arthropod abundance, species richness and community composition. We asked the following two research questions: (1) How does increasing configurational crop heterogeneity by strip cropping single species and cultivars influence the abundance and species richness of aerial arthropod communities compared to large scale monocultures? and (2) How does increasing compositional crop heterogeneity by the addition of plant species within strips influence the abundance, species richness, and community composition of plant and aerial arthropod communities? Our results contribute to an increased understanding of aerial arthropod community responses to strip cropping in large scale agricultural landscapes, as a basis for design of field-level

crop diversification management options.

2. Materials and methods

2.1. Experimental site and set-up

The study was conducted in a long-term strip cropping experiment on the experimental organic arable farm of Wageningen University and Research in Flevoland province, The Netherlands (52°32'44.4"N 5°34'12.5"E). The farm is located on a homogeneous sandy clay loam soil (Fluvisol on marine sediment, 17% clay) of up to 1.2 m soil depth. The region is characterized by intensive, large scale arable crop production with average field sizes of 20 ha. In Flevoland 66% of all land is used by agriculture (CBS, 2022). On-farm semi-natural elements cover less than 4% of the farmed area (Manhoudt and de Snoo, 2003) and consist of water ways with grassy vegetation, sparse hedgerows, occasional annual and perennial flower banks, and farmyard trees.

The experiment was conducted as part of a multi-year system experiment (Drinkwater, 2002). Two strip cropping fields (80 x 250 m) were established as replicates (Supplementary materials Figure S.1.1.). The strip cropping fields were bordered on their north and south sides by 3-meter-wide perennial flower strips (for full species list see Supplementary materials Table S.2.1.). Both strip cropping fields included the crop pairs cabbage - wheat and sugar beet - barley. Each crop pair included two strip cropping configurations (hereafter called "treatments"): (i) 3-meter wide strips in which multiple rows of a single crop species were sown (*STRIP*), and (ii) as in *STRIP* but with eight additional plant species sown into the grain strip of the crop pair in an additive design (*STRIPMIX*) (Fig. 1B). Each strip had an area of approximately 190 m² (60 m x 3.15 m). Each treatment was replicated three times and therefore contained six crop strips, consisting of three strips of each crop. Four out of the six strips were used for sampling (Fig. 1C). In the *STRIPMIX* treatment, barley strips were mixed with, among others, *Pisum sativum*, while wheat strips were mixed with, among others, *Vicia faba* (for full species list see Supplementary materials Table S.2.1.).

Monocultural cabbage fields (treatment *MONO*) were included as a reference (Fig. 1A; Supplementary materials Figure S.1.1.). In 2019, *MONO* (40 m x 60 m) was located next to strip cropping field 2, while in 2020, a new *MONO* cabbage field (280 m x 174 m) was selected, which was located in between the two strip cropping fields (Supplementary materials Figure S.1.1.). Adjacent to the monoculture fields, 3-meter wide wheat and cabbage strips (*STRIP*) were added to enable statistical comparison based on an incomplete block design (Fig. 1; Supplementary materials Figure S.1.1.).

2.2. Aerial arthropod sampling

Aerial arthropod communities in the *STRIP* and *STRIPMIX* treatments were assessed by sweep netting 50 m transects, excluding the first 5 m near the headlands. Transect sampling involved walking back and forth along the edge of a crop strip, sampling the 1.5 m towards the center of the 3 m strip for a total sampling area of 150 m² per strip, within an allocated sampling time of 15 min. The two strips bordering other treatments were excluded from sampling to avoid border effects (Fig. 1, Supplementary materials Figure S.1.2.). The reference monocrop treatment *MONO* was sampled in the middle of the field by walking similar transects as in the strips (Supplementary materials Figure S.1.3.). Sampling was conducted with a white 30 cm diameter sweepnet (®Vermandel) under dry, sunny, and low-wind conditions with temperatures ranging between 17 °C and 30 °C. In 2019, cabbage - wheat and sugar beet - barley were sampled in two rounds in July (1st or 3rd and 22nd or 23th or 24th), for a total of 72 transects. In 2020, cabbage - wheat was sampled in three rounds in June (19th), July (23rd) and August (18th), for a total of 66 transects (Table 1). Hence, 138 transects were sampled in total (Supplementary materials Table S.3.1.).

Collected arthropods were identified in the field up to species level

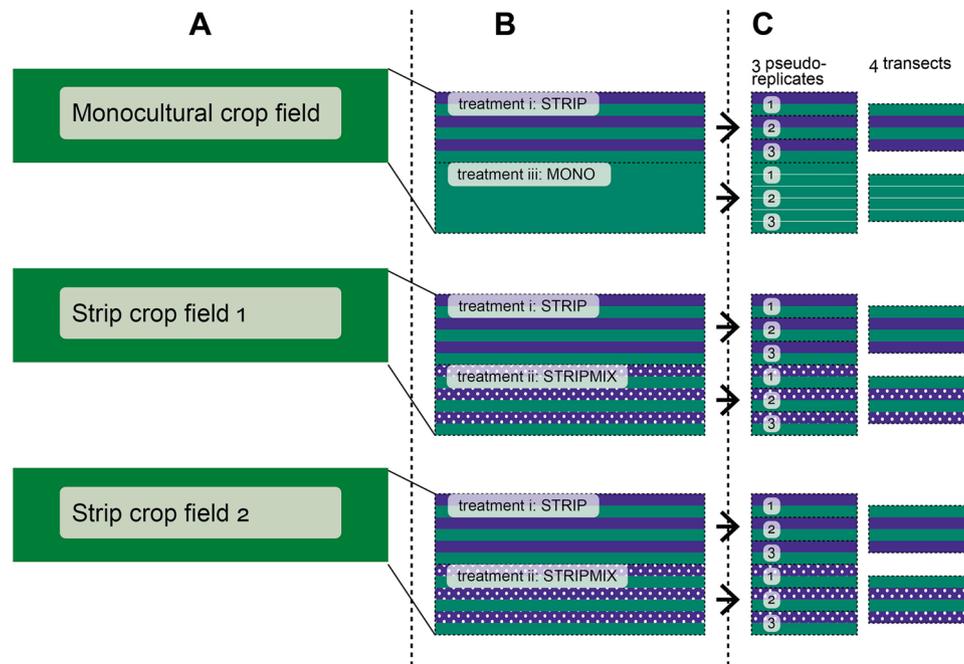


Fig. 1. Schematic overview of the experimental design. The monocultural crop field (A) contained a monocultural cabbage treatment (*MONO*) and a cabbage - wheat strip cropping treatment (*STRIP*). Strip cropping field 1 and 2 (A) were replicates and included two treatments: i: *STRIP* and ii: *STRIPMIX*. Each treatment contained six crop strips, three of each crop (B). Four out of the six crop strips were sampled (C), excluding the border crop strips. The same design was applied in both years.

Table 1

Overview of aerial arthropod and vegetation sampling effort in different crops and treatments: monocultural crop fields (*MONO*), 3 m wide strips of a single crop species (*STRIP*), and the same as in *STRIP* but with additional plant species sown into the grain strip in an additive design (*STRIPMIX*). In all crops aerial arthropods were sampled. Crops indicated with (*) were also sampled for associated vegetation. Additional information on sampling effort per treatment: [Supplementary materials Table S.3.1.](#) & [S.3.2.](#)

	Year	
Treatments	2019	2020
	#Rounds: 2	#Rounds: 3
	Sampling month: July	Sampling months: June, July, August
<i>MONO</i>	Cabbage	Cabbage
<i>STRIP</i>	Cabbage*; wheat* Sugar beet*; barley*	Cabbage*; wheat*
<i>STRIPMIX</i>	Cabbage*; wheat* Sugar beet*; barley*	Cabbage*; wheat*

(apidae, syrphidae, piridae, nymphalidae, noctuidae, coenagrionidae, libellulidae, acrididae), up to genus level (tipulidae, plutellidae) or up to family level (cantharidae, coccinellidae, parasitica, tenthredinidae, chrysopidae). Unidentified specimens were collected in a killing jar and taken to the laboratory for identification. Larval and adult stages of coccinellidae and of *Pieris rapae* were recorded separately. When *P. xylostella* adult abundance was less than 100 individuals per transect all individual moths were counted. At higher *P. xylostella* abundances (>100 individuals/transect) the number was estimated (see [Supplementary materials Table S.4.1.](#) for full species list).

2.3. Monitoring of associated vegetation

The associated vegetation (i.e. spontaneously established plant species associated with the crop, also referred to as ‘weeds’, plus additionally sown plant species) was assessed in rectangular vegetation plots of 3 m x 5 m ([Mueller-Dombois and Ellenberg, 1974](#); [Chytrý and Preislerová, 2003](#)). The plots were established in the same strips as used for aerial arthropod sampling. Two plots per strip were sampled. Associated

vegetation was not assessed in *MONO* because this treatment was located on fields which had a different cropping history and weed seed bank as the *STRIP* and *STRIPMIX* treatments and were therefore not comparable in terms of associated plant communities. The first and last 5 m of the strips were not sampled to avoid edge effects from the headlands. All vascular plant species were recorded and identified up to species level ([Supplementary materials Table S.4.3.](#)), and their abundance was recorded using the Tansley scale ([Tansley, 1946](#)), discriminating between flowering and non-flowering individuals. The assessments were conducted in cabbage - wheat and sugar beet - barley in 2019, and cabbage - wheat in 2020 ([Table 1](#)). In 2019, 64 assessments were made in two rounds in July (1st or 2nd and 29th or 30th) and in 2020, 60 assessments in three rounds in June (25th), July (28th) and September (22nd), for a total of 124 vegetation plots in both years ([Supplementary materials Table S.3.2.](#)). The vegetation data were stored and managed with the software package Turboveg 2.0 ([Hennekens and Schaminée, 2001](#)).

2.4. Statistical analysis

To analyze the effect of the strip cropping configuration on aerial arthropod and vegetation abundance, species richness and community composition, a combination of univariate and multivariate statistics was used. For the first research question we tested the effects of configurational crop heterogeneity (*MONO* vs. *STRIP*) on aerial arthropod communities in cabbage using generalized linear models (GLM's). In this first analysis, we analyzed the effects of treatment, sampling round, and their two-way interactions (explanatory variables) on the following response variables: (i) total arthropod abundance, (ii) total arthropod species richness, (iii) Shannon diversity index, (iv) herbivore abundance, (v) herbivore species richness, (vi) natural enemy abundance, and (vii) natural enemy species richness. As diamondback moth (*P. xylostella*) had been estimated rather than counted in one sampling round, we also ran the analysis after removing *P. xylostella* (viii). We used two-year field data, and we gave each round a unique ID resulting in five sampling round levels. For the second research question, we tested the effects of compositional crop heterogeneity (*STRIP* vs.

STRIPMIX) on aerial arthropod and plant communities in cabbage – wheat and sugar beet – barley strip cropping of 2019 using a second GLM. In this second analysis, we analyzed the effects of treatment, sampling round, field (field 1 and field 2) and crop, and their two-way interactions on the same response variables as in the first model and additionally (ix) total vegetation abundance, (x) total vegetation species richness, (xi) flowering plant abundance, and (xii) flowering plant species richness.

For count data a Poisson error distribution was used unless there was overdispersion. In the latter cases we tested a generalized Poisson distribution or negative binomial error distribution (Consul and Famoye, 1992). In all analyses we used model selection, which was performed using the ‘dredge’ function accessed through package *MuMin* (Bartoń, 2020) on the full model and ranked the output by AIC. As there were often multiple candidate models within Δ AIC < 2, we chose the model which included treatment as explanatory variable. If there were multiple models within Δ AIC < 2 including treatment, we selected the model with the lowest AIC as the final model. To check model assumptions, we inspected the scaled residuals from the fitted model using function ‘simulateResiduals’, visually inspected QQ plot residuals, and tested for zero inflation using function ‘testZeroInflation’, all accessed using package *DHARMA* (Hartig, 2021). To test whether any of the explanatory variables significantly explained variation in the response variables we used a Type II Wald chi-squared test using the function ‘anova’ accessed through the package *car* (Fox and Weisberg, 2018). Whenever treatments significantly affected the response variables (Wald $\chi^2 \leq 0.05$), we performed a pairwise comparison using Tukey HSD test.

Multivariate analyses were used to test effects of treatment, crop, and sampling round on aerial arthropod and plant community composition. For this purpose we used the 2019 dataset with the *STRIP* and *STRIPMIX* treatments of both the cabbage - wheat and sugar beet - barley crop pairs. We calculated the Bray-Curtis dissimilarity using the raw abundance arthropod and plant data to attain a distance matrix. To avoid negative eigenvalues we applied a square root transformation on the distance matrix before we run a Principal Coordinate Analyses (PCoA) for each arthropod community and plant community separately. We calculated the proportion of explained variation by different axes and determined the optimal number of PCoA axes using a visual assessment of scree plots (Cattell, 1966). Then we assessed relationships between explanatory variables (crop, sampling round, treatment, field) and PCoA axes. Finally, we assessed whether the different crops and treatments had distinct arthropod communities with PerMANOVA using function ‘pairwise.adonis2’ accessed through package *vegan* (Oksanen et al., 2017). Significant differences between communities in crop and treatments were assessed by assessing the $P = 0.05$ level. All statistical analyses were performed in R (version 3.6.1) accessed through RStudio (R Development Core Team, 2020). Packages used include *ape* (Paradis et al., 2004), *car* (Fox and Weisberg, 2018), *DHARMA* (Hartig, 2021), *emmeans* (Lenth, 2021), *ggplot2* (Wickham, 2016), *glmmTMB* (Brooks et al., 2017), *multcomp* (Hothorn et al., 2008), *MuMin* (Bartoń, 2020) and *vegan* (Oksanen et al., 2017).

3. Results

3.1. Aerial arthropod and plant species pool

In the 138 transects we counted 10,692 aerial arthropod individuals, 1000 individuals in 2019 and 9692 in 2020, and found a total species richness of 31, covering seven orders (Supplementary materials Table S.4.1. & S.4.2.). Overall, *P. xylostella* (diamondback moth) made up the bulk of all arthropod individuals (84%). Particularly in the first round in 2020, *P. xylostella* was abundant (± 400 individuals/transect). In the 124 plant transects 1542 individual plants were counted, 790 in 2019 and 752 in 2020, with a total species richness of 48, covering 10 orders (Supplementary materials Table S.4.1. & S.4.3.). Purposefully sown annual plant species in the grain crop strips comprised 188 individual

plants, including *Vicia faba* (85 individuals) and *Pisum sativa* (35 individuals). Of the 10 additionally sown plant species in *STRIPMIX* (Supplementary materials Table S.2.1.), one was not encountered in the transect walks (*Silene noctiflora*). Overall, Caryophyllales made up the bulk of all plant individuals (50%) with *Stellaria media* (chickweed) being the most abundant plant species (290 individuals).

3.2. Aerial arthropod abundance and species richness in STRIP vs. MONO

Total arthropod abundance and herbivore abundance across the five sampling rounds was significantly lower in the 3 m wide cabbage strips than in the monoculture reference ($p = 0.017$ and $p = 0.015$, Table 2, Fig. 2). However, when *P. xylostella* was excluded from the data the differences between *STRIP* and *MONO* were not significant anymore (Table 2). In 2019, the abundance of *P. xylostella* was low in the first sampling round in all treatments and increased 2.5 times in the *MONO* treatment in round two, but not in *STRIP* (Fig. 3). In 2020, a similar pattern was observed, even though *P. xylostella* already reached a high abundance in *MONO* in round one. Natural enemy communities in cabbage were dominated by coccinellidae and syrphidae (Fig. 3). Natural enemy abundance was not significantly different between cabbage *STRIP* and *MONO* (Table 2). Total arthropod species richness and herbivore species richness in cabbage were not significantly influenced by strip cropping. In contrast, natural enemy species richness was significantly higher in cabbage grown in strips than in cabbage grown in monocultures ($p = 0.008$, Table 2, Fig. 2).

3.3. Aerial arthropod abundance, species richness and community composition in STRIP vs. STRIPMIX

3.3.1. Aerial arthropod abundance and species richness

Total arthropod abundance was significantly higher in *STRIPMIX* compared to *STRIP* ($p = 0.003$; Table 3), also when *P. xylostella* was excluded (Table 3). Total arthropod species richness was significantly enhanced in *STRIPMIX* by 21% compared to *STRIP* ($p = 0.018$; Table 3). The Shannon diversity index and natural enemy abundance were significantly higher in *STRIPMIX* than in *STRIP* ($p = 0.019$ and $p = 0.028$, respectively).

3.3.2. Aerial arthropod community composition

The first PCoA axis was mainly related to crop species and to a lesser extent to the presence of additional sown plant species and explained 14.3% of the variation in aerial arthropod community composition (Fig. 4). The second axis was associated with sampling round (11.1% explained variation). PCoA axis one was positively associated with two specialist cabbage herbivores: *P. xylostella* (diamondback moth) and *Pieris rapae* (cabbage white). PCoA axis two was negatively associated with Coccinellidae and several Syrphidae species (Supplementary materials, Figure S.5.3.). Aerial arthropod community composition was significantly different between crops ($p < 0.001$) and rounds ($p < 0.001$). Significant differences in aerial arthropod communities between *STRIP* and *STRIPMIX* were only found for barley ($p < 0.05$) (Table 4).

3.4. Plant abundance, species richness and community composition in STRIP vs. STRIPMIX

3.4.1. Plant abundance and species richness

Total plant abundance and total plant species richness were significantly higher in *STRIPMIX* than in *STRIP* ($p < 0.001$ and $p = 0.008$, respectively; Table 3, Fig. 5), in both the cabbage – wheat and sugar beet – barley combination (Supplementary materials Table S.6.1. & S.6.2.). Total plant abundance was 33% higher in *STRIPMIX* (14 plants per vegetation plot of 150 m²) than in *STRIP* (11 plants per vegetation plot) when averaged across all four crops (Table 3). In *STRIPMIX*, additionally

Table 2

Results of model selection to elucidate effects of treatments *STRIP* and *MONO* and round on aerial arthropod abundance and species richness using data of cabbage in 2019 and 2020. Response variables included total arthropod abundance, total arthropod abundance excluding *P. xylostella*, total arthropod species richness, Shannon index, herbivore abundance, herbivore abundance excluding *P. xylostella*, herbivore species richness, natural enemy (NE) abundance and natural enemy species richness. Error distributions, explanatory variables, χ^2 , p-value, direction of treatment effect and parameter estimates (Est.) and their 95% confidence interval (CI) are indicated. Significance levels of effects were obtained by p-values between response variable and explanatory variable treatment resulting from ANOVA test; * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$. Response variables depicted in italics have a significant treatment effect in Tukey HSD post-hoc tests.

Resp. variable	Error distribution ^a	Expl. variables	χ^b	p	Treatment effect	Treatment	Est.	CI
<i>Arthropods</i>								
<i>Total abundance</i>	Nbinom2	Round ***	1669.664	< 0.001	STRIP < MONO	STRIP	177	157–197
		Treatment *	5.738	0.017		MONO	195	173–216
		Round:treatment **	13.466	0.009				
<i>Total abundance excl. P. xylostella</i>	Nbinom2	Round ***	65.848	< 0.001	n.s.	STRIP	22	4–39
		Treatment	0.027	0.871		MONO	21	7–35
<i>Total species richness</i>	Genpois	Round ***	64.311	< 0.001	n.s.	STRIP	3.02	2.71–3.33
		Treatment	2.279	0.132		MONO	2.69	2.43–2.95
		Round:treatment **	18.024	0.001				
<i>Shannon index</i>	Genpois	Round	3110229	< 0.001	na ^b	na	na	na
<i>Herbivore abundance</i>	Nbinom2	Round ***	1478.091	< 0.001	STRIP < MONO	STRIP	175	154–196
		Treatment *	5.897	0.015		MONO	195	171–216
		Round:treatment **	22.752	0.0001				
<i>Herbivore abundance excl. P. xylostella</i>	Nbinom2	Round ***	65.609	< 0.001	n.s.	STRIP	18	1–37
		Treatment	0.073	0.787		MONO	20	2–39
<i>Herbivore species richness</i>	Genpois	Round **	15.531	0.004	n.s.	STRIP	1.71	1.47–1.94
		Treatment	0.144	0.704		MONO	1.81	1.58–2.03
		Round:treatment **	28.448	< 0.001				
<i>NE abundance</i>	Poisson	Round	6.421	0.167	n.s.	STRIP	1.03	0.83–2.57
		Treatment	1.916	0.166		MONO	1.70	0.46–1.61
<i>NE species richness</i>	Genpois	Round *	11.053	0.026	STRIP > MONO	STRIP	0.82	0.57–1.08
		Treatment **	6.990	0.008		MONO	0.47	0.33–0.61

^a Nbinom2: negative binomial distribution with a quadratic parameterization, Genpois: generalized Poisson distribution, Poisson: Poisson distribution.

^b In model selection, treatment was not selected as explanatory variable.

sown plant species comprised 24% of total plant counts in the vegetation plots (data not presented), whilst the other 76% of the plant counts included spontaneously established plant species (weeds). When removing the additionally sown plant species from the dataset, no significant differences in plant abundance and plant species richness were detected between *STRIP* and *STRIPMIX* (data not presented). Thus, the total abundance and richness of flowering plants were not influenced by *STRIPMIX* (Table 3, Fig. 5) in neither the cabbage – wheat combination nor the sugar beet – barley combination (Supplementary materials Table S.6.1. & S.6.2.).

3.4.2. Plant community composition

The first PCoA axis was related to field and explained 19.8% of the variation in plant community composition. The second axis was associated with crop type (8.8% explained variation). PCoA axis one was negatively associated with *Polygonum aviculare* (common knotgrass) and *Chenopodium ficifolium* (fig-leaved goosefoot) and positively associated with *Persicaria maculosa* (redshank). PCoA axis two was positively associated with *Vicia faba* (Supplementary materials, Figure S.5.2.). Plant community composition was significantly different between crops ($p < 0.001$), sampling rounds ($p = 0.035$) and treatments *STRIP* and *STRIPMIX* in wheat ($p < 0.001$) and barley ($p < 0.001$) (Table 4).

4. Discussion

We assessed how arthropod and plant communities were influenced by increased configurational crop heterogeneity (by strip cropping) and compositional crop heterogeneity (by sowing additional plant species in strips). We present four key findings. First, total aerial arthropod and herbivore abundances were higher in monoculture cabbage fields than in strip cropped cabbage fields. Second, natural enemy species richness was lower in monoculture cabbage fields than in strip cropped cabbage fields. Third, the addition of plant species in wheat and barley strips led to significantly higher total arthropod abundances, natural enemy abundance and total arthropod species richness compared to strip

cropped fields without additionally sown plant species in grain crop strips. Fourth, there were significant differences in plant community composition among the crops and between the strips with and without additionally sown plant species. However, additional plant species sown within strips did not significantly affect the arthropod community composition, except in barley.

4.1. Effect of configurational crop heterogeneity on aerial arthropod communities

We found that strip cropping cabbage can reduce herbivore pressure in general and *P. xylostella* in particular. The results align with previous studies that report positive effects of intercropping on pest suppression (Tonhasca and Byrne, 1994; Finch and Kienegger, 1997; Åsman et al., 2001; Hambäck et al., 2009) and specifically on suppressing *P. xylostella* in Brassicaceae crops (Åsman et al., 2001; Bukovinszky et al., 2004; Tajmiri et al., 2017). Reduced *P. xylostella* abundance in cabbage strips combined with wheat strips can be explained by at least two ecological mechanisms. First, strip cropping may have disrupted the host plant finding by *P. xylostella*, leading to lower oviposition and *P. xylostella* abundance in strip cropped cabbage fields (Andow, 1991; Finch and Collier, 2000; Åsman et al., 2001). Our findings on the apparent suppression of cabbage specialist *P. xylostella* by strip cropping are in line with findings of Juventia et al. (2021) who reported a negative association between crop diversity and feeding injury in organically managed (strip) crop systems, and a meta-analysis showing that specialist herbivores respond negatively to plant diversity, particularly at small spatial scales (Dassou and Tixier, 2016). A second ecological mechanism which may explain the reduced herbivore populations in strip cropped cabbage in our study is enhanced top-down control by natural enemies, which can benefit from increased plant diversity (Barnes et al., 2020). However, natural enemy abundance in strip cropped cabbage fields was not significantly different than in monoculture cabbage fields during the five sampling rounds. Nevertheless, we cannot exclude the possibility that our sampling methodology was not effective in the collection of some

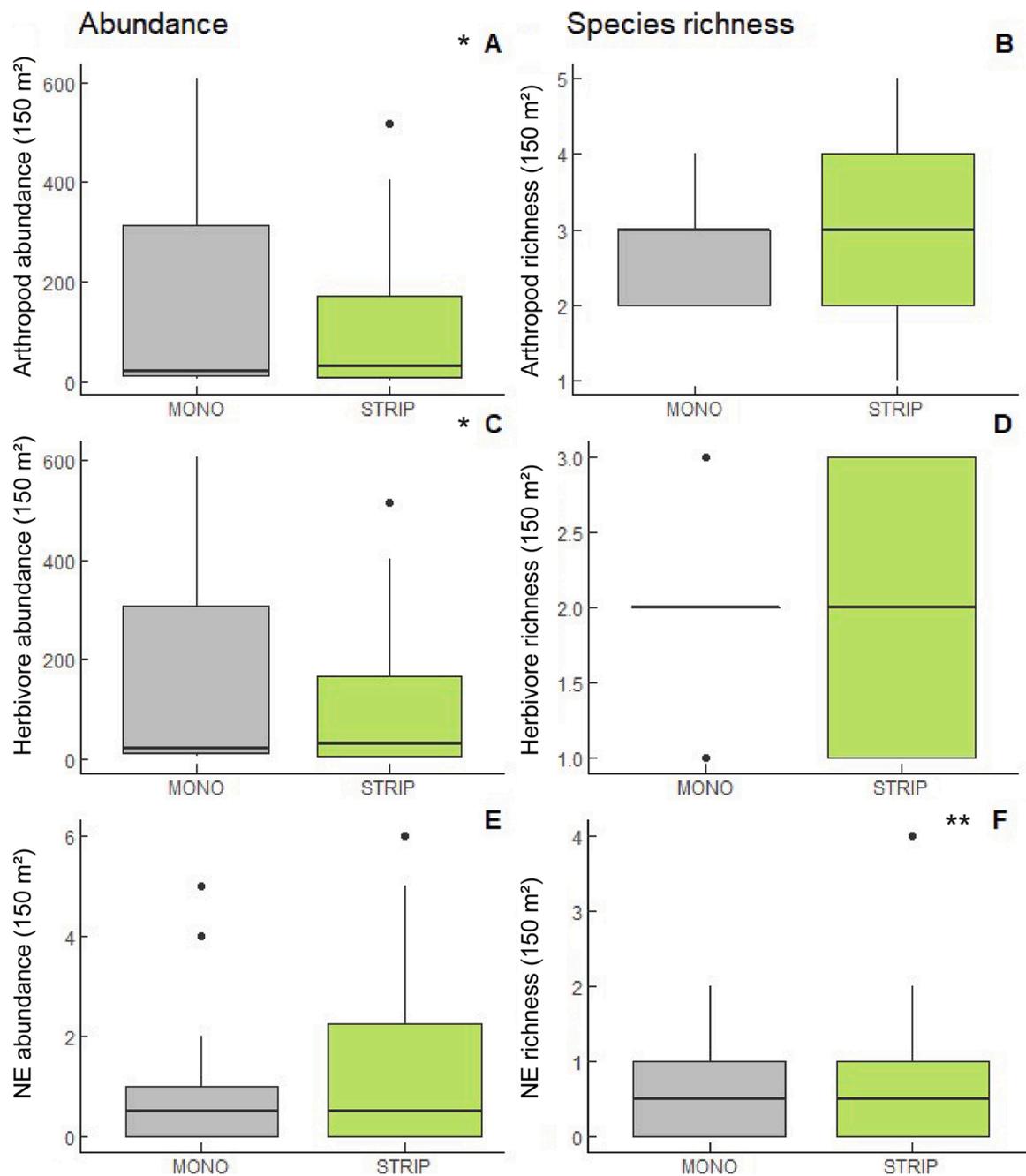


Fig. 2. Abundance and species richness of the aerial arthropod community, herbivore community and natural enemy community (NE) during five sampling rounds across two years. Left panels (A, C, E): arthropod abundance (A), herbivore abundance (C), and natural enemy abundance (E). Right panels (B, D, F): arthropod species richness (B), herbivore richness (D), and natural enemy richness (F) obtained by sweet netting cabbages in monocultures (*MONO*) and cabbage strips adjacent to wheat strips (*STRIP*). *MONO* consisted of a cabbage monoculture of 0.24 ha (2019) and 4.9 ha (2020). Asterisks indicate significant levels of treatments: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (Table 2).

important natural enemies of *P. xylostella*, such as minute egg parasitoids, which have the potential to effectively suppress Lepidopteran pests (Philips et al., 2014). Additional sampling methodologies could provide more insight in the potential of strip cropping for enhanced biocontrol in future experiments.

Contrary to natural enemy abundance, natural enemy species richness was significantly higher in strip cropped cabbage fields compared to monocultural cabbage fields. This finding aligns with the main outcomes of meta-analyses assessing effects of plant diversity on herbivore and predator communities (Letourneau et al., 2011; Dassou and Tixier, 2016). In the meta-analysis of Dassou and Tixier (2016), both predator abundance and predator diversity were significantly higher in more

diverse plant assemblages. Letourneau et al. (2011) found a 44% greater abundance of natural enemy populations in diversified fields as opposed to monocultures. Recent studies provided insights on responses of ground-dwelling natural enemy communities to narrow and wide strip cropping fields. Alarcón-Segura et al. (2022) did not find higher ground-dwelling natural enemy richness in wheat and oilseed rape strips (27 and 36 m) as compared to monocultures. In contrast, Ditzler et al. (2021) found significantly higher richness and evenness of ground-dwelling natural enemies of aphids in wheat strips (3 and 6 m) compared to wheat monocultures. The increased natural enemy species richness in strip cropped cabbage in our study (3 m strips) can be mostly attributed to Cantharidae, Coccinellidae, and Syrphidae species

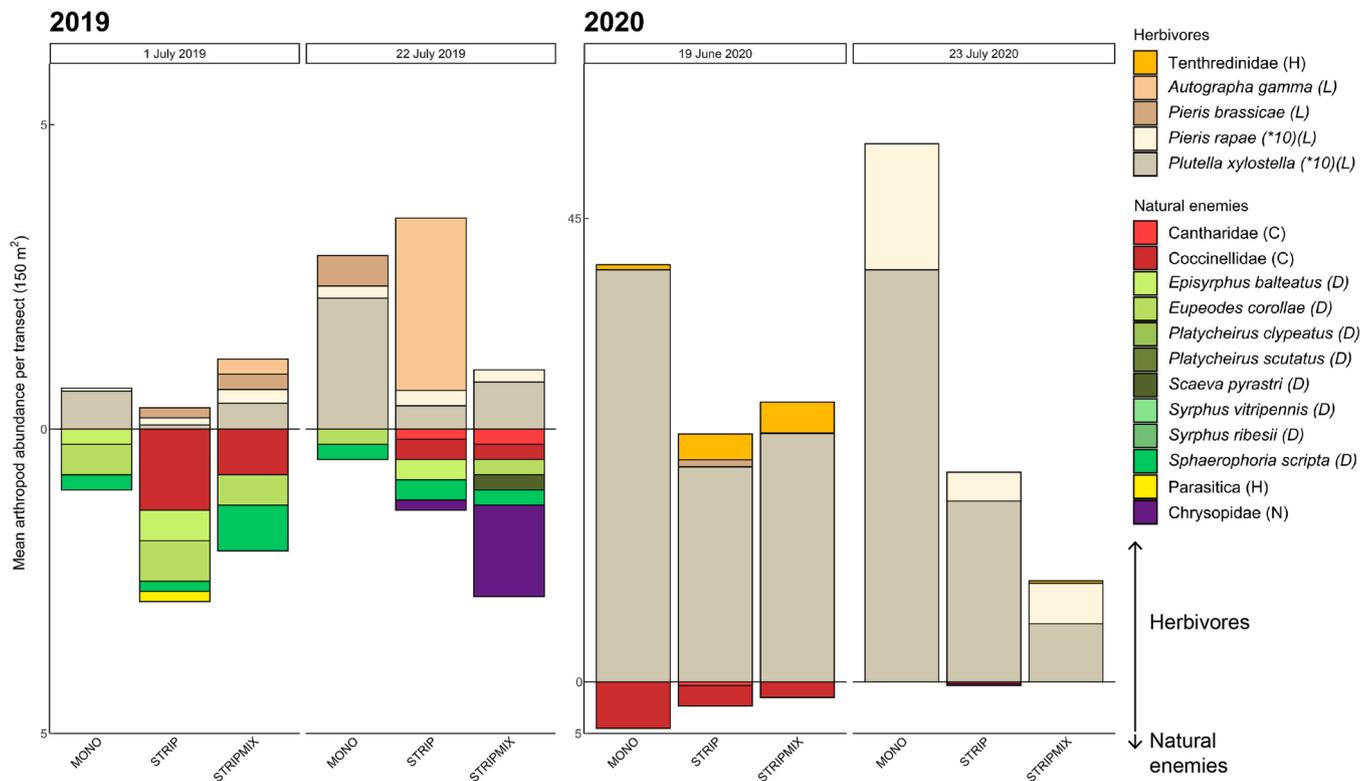


Fig. 3. Herbivore (↑ y-axis) and natural enemy (↓ y-axis) community composition. Samples were collected by sweep netting transect walks in cabbage monocultures (MONO) in two different strip cropping treatments: 3 m wide cabbage strips alternated with 3 m wide wheat strips (STRIP), and 3 m wide cabbage strips alternated with 3 m wide wheat strips with additional sown plant species (STRIPMIX). MONO refers to a cabbage monoculture of 0.24 ha (2019) and 4.9 ha (2020). Capital letters after arthropod species names in the legend indicate arthropod orders: Hymenoptera (H), Lepidoptera (L), Coleoptera (C), Diptera (D) and Neuroptera (N). Only herbivore and natural enemy species are shown. *Plutella rapae* and *P. xylostella* numbers are divided by 10 to increase readability of the figure. A figure with standard scaling is presented in [Supplementary materials S.5.1](#). Bars indicate mean arthropod numbers of multiple transects for two rounds in two consecutive years (2019; 2020). The third round in 2020 has been left out because too few arthropods were found for meaningful visualization ([Supplementary materials Table S.3.1](#)).

associated with wheat crop strips, which spilled over into cabbage strips. This suggests that these spill-over effects take place at relatively small spatial scales and can be detected in relatively narrow, but not in wide strips. Our work adds to the large body of studies showing how herbivore populations are affected by field size and crop diversification including strip cropping (Martin et al., 2019). However, we did not find evidence for increased top-down control by natural enemies. Therefore, bottom-up effects are the most plausible explanation for the reduced pest density in strip cropped cabbage fields in our study, corresponding to earlier findings in a meta-analysis by Vidal and Murphy (2018), who showed that chewing herbivores were more affected by bottom-up forces than by top-down forces.

4.2. Effect of compositional crop heterogeneity on aerial arthropod and plant communities

The addition of plant species to grain crop strips led to significantly higher total arthropod abundance, natural enemy abundance, and total arthropod species richness, which aligns with findings of other studies (Dassou and Tixier, 2016; Wan et al., 2020; Brandmeier et al., 2021). Brandmeier et al. (2021) studied arthropod communities in monocultures and mixtures of spring wheat and faba bean and found that increased crop diversity nearly always led to higher arthropod abundance and richness, promoting richness stronger than abundance. Contrary to Brandmeier et al. (2021) who used a replacement design, we used an additive design (Snaydon, 1991) by sowing several rare additional plant species in STRIPMIX. While this sowing strategy resulted in a higher plant species richness than STRIP, the flower cover in STRIPMIX was not different from STRIP. Nevertheless, aerial arthropod abundance

and species richness were significantly higher in STRIPMIX than in STRIP. For instance, Syrphidae were more abundant in wheat and barley STRIPMIX than in STRIP, and Coccinellidae were more abundant in the wheat STRIPMIX than in STRIP. Most likely, the *Vicia faba* that was included in the wheat STRIPMIX treatment provided extrafloral nectar resources and abundant prey (black bean aphids, *Aphis fabae*), and attracted aphidophagous Syrphidae and Coccinellidae species (Weber and Lundgren, 2009; Serée et al., 2022). *Pisum sativum*, which was sown in the barley STRIPMIX, also provided floral food resources and possibly prey, but most likely to a lesser extent than *Vicia faba*. Increasing floral resources, flower cover and flower diversity in STRIPMIX might be key to gaining insights in the full potential of this diversification strategy in supporting farmland arthropod biodiversity.

We found that different crop types support significantly distinct plant and arthropod communities. Crop-specific associated plant community compositions have earlier been reported by Hofmeijer et al. (2021), and can be explained by the specific resource, disturbance, shading and micro-climate conditions within different crops (Storkey and Neve, 2018). The effect of crop type on plant community composition implies that strip cropping can increase biodiversity at larger spatial scales (i.e., higher β -diversity). Differences in aerial arthropod community composition among crops may be explained by the specific type, quantity, quality and timing of resources provided by crops and their associated plants (Meyer et al., 2019). The additional sown plant species in STRIPMIX did not generally lead to clearly altered arthropod community composition compared to STRIP, except for barley, for which the arthropod community in STRIPMIX barley became more similar to the arthropod community in sugar beet (Fig. 4). This suggests that the arthropod community in sugar beet in STRIPMIX spilled over into the

Table 3

Results of model selection to elucidate effects of treatment (*STRIP* and *STRIPMIX*), crop, round and field on aerial arthropod and plant abundance and species richness using data of cabbage – wheat and sugar beet – barley in 2019. Response variables included total arthropod abundance, total arthropod abundance excl. *P. xylostella*, total arthropod species richness, Shannon index, herbivore abundance, herbivore abundance excluding *P. xylostella*, herbivore species richness, natural enemy (NE) abundance, natural enemy species richness, total plant abundance, plant species richness, flowering plant abundance and flowering plant species richness. All response variable regarding plant abundance and plant species richness include additional plant species sown in strips and spontaneously established plant species (weeds). Error distributions, explanatory variables, χ^2 , p-value, direction of treatment effect and parameter estimates (Est.) and their 95% confidence interval (CI) are indicated. Significance levels of effects were obtained by p-values between response variable and explanatory variable treatment resulting from ANOVA test; * indicates p < 0.05, ** indicates p < 0.01, *** indicates p < 0.001. Response variables depicted in italics have a significant treatment effect in Tukey HSD post-hoc tests.

Resp. variable	Error distribution ^a	Expl. variables	χ^2	p	Treatment effect	Treatment	Est.	CI
<i>Arthropods</i>								
<i>Total abundance</i>	Nbinom2	Crop *** Field Round Treatment ** Field:treatment ** Round:treatment *	25.054 0.600 0.024 8.786 6.784 4.421	< 0.001 0.438 0.876 0.003 0.009 0.035	STRIPMIX > STRIP	STRIP STRIPMIX	11.00 15.90	8.79–13.2 13.04–18.8
<i>Total abundance excl. P. xylostella</i>	Nbinom2	Crop *** Field Round Treatment ** Field:treatment * Round:treatment *	47.614 0.112 0.505 6.837 4.938 4.914	< 0.001 0.738 0.477 0.009 0.026 0.027	STRIPMIX > STRIP	STRIP STRIPMIX	10.00 14.20	8.06–12.0 11.63–16.8
<i>Total species richness</i>	Genpois	Crop *** Field Round * Treatment * Field:treatment **	24.384 0.932 4.064 5.559 8.933	< 0.001 0.334 0.044 0.018 0.003	STRIPMIX > STRIP	STRIP STRIPMIX	4.38 5.30	3.87–4.90 4.73–5.87
<i>Shannon index</i>	Genpois	Round Treatment *	0.008 5.473	0.930 0.019	STRIPMIX > STRIP	STRIP STRIPMIX	1.17 1.30	1.06–1.29 1.18–1.43
<i>Herbivore abundance</i>	Poisson	Crop *** Field ** Round *** Treatment Crop:treatment * Field:treatment *Round:treatment ***	91.3298.08111.0610.7759.6286.60714.339	< 0.0010.0040.0010.3790.0220.010 < 0.001	n.s.	STRIPSTRIPMIX	2.943.34	2.33–3.552.70–3.99
<i>Herbivore abundance excl. P. xylostella</i>	Poisson	Crop ***Field Round Treatment Crop:treatment Field:treatment Round:treatment ***	30.2630.3722.5420.1277.4323.02415.940	< 0.0010.5420.1110.7210.0590.082 < 0.001	n.s.	STRIPSTRIPMIX	1.841.94	1.36–2.331.44–2.43
<i>Herbivore species richness</i>	Genpois	Crop ***Field *Round Treatment Crop:treatment * Field:treatment *** Round:treatment ***	44.35510.7910.5900.30714.14024.57124.910	< 0.0010.0010.4420.5790.003 < 0.001 < 0.001	n.s.	STRIPSTRIPMIX	1.051.11	0.93–1.170.98–1.23
<i>NE abundance</i>	Genpois	Crop ***Field Round Treatment *	32.4730.4285.5854.804	< 0.0010.5130.0180.028	STRIPMIX > STRIP	STRIPSTRIPMIX	7.510.9	5.45–9.558.36–13.39
<i>NE species richness</i>	Genpois	Crop ***Round Treatment ***	33.39614.7281.222	< 0.001 < 0.0010.269	n.s.	STRIPSTRIPMIX	2.693.00	2.30–3.082.59–3.41
<i>Vegetation Total abundance</i>	Poisson	Crop ***Field **Round Treatment ***Crop:treatment **Round:treatment *	35.11229.6331.78815.12817.5664.575	< 0.001 < 0.0010.181 < 0.001 < 0.0010.032	STRIPMIX > STRIP	STRIPSTRIPMIX	10.614.1	9.41–11.712.79–15.5
<i>Total species richness</i>	Genpois	Crop *Field ***Round Treatment **Crop:treatment * Field:treatment **Round:treatment **	15.67953.5050.0407.00212.4114.521	0.001 < 0.0010.8410.0080.0060.033	STRIPMIX > STRIP	STRIPSTRIPMIX	5.326.43	4.79–5.855.85–7.02
<i>Flowering total abundance</i>	Genpois	Crop ***Field RoundTreatment	28.16015.4672.5091.013	< 0.001 < 0.0010.1130.314	n.s.	STRIPSTRIPMIX	3.073.43	2.59–3.562.91–3.94
<i>Flowering total sp. richness</i>	Genpois	Crop ***Field **Round Treatment	20.59523.3615.2350.848	< 0.001 < 0.0010.0220.358	n.s.	STRIPSTRIPMIX	2.833.11	2.41–3.252.67–3.55

^a Nbinom2: negative binomial distribution with a quadratic parameterization, Genpois: generalized Poisson distribution, Poisson: Poisson distribution.

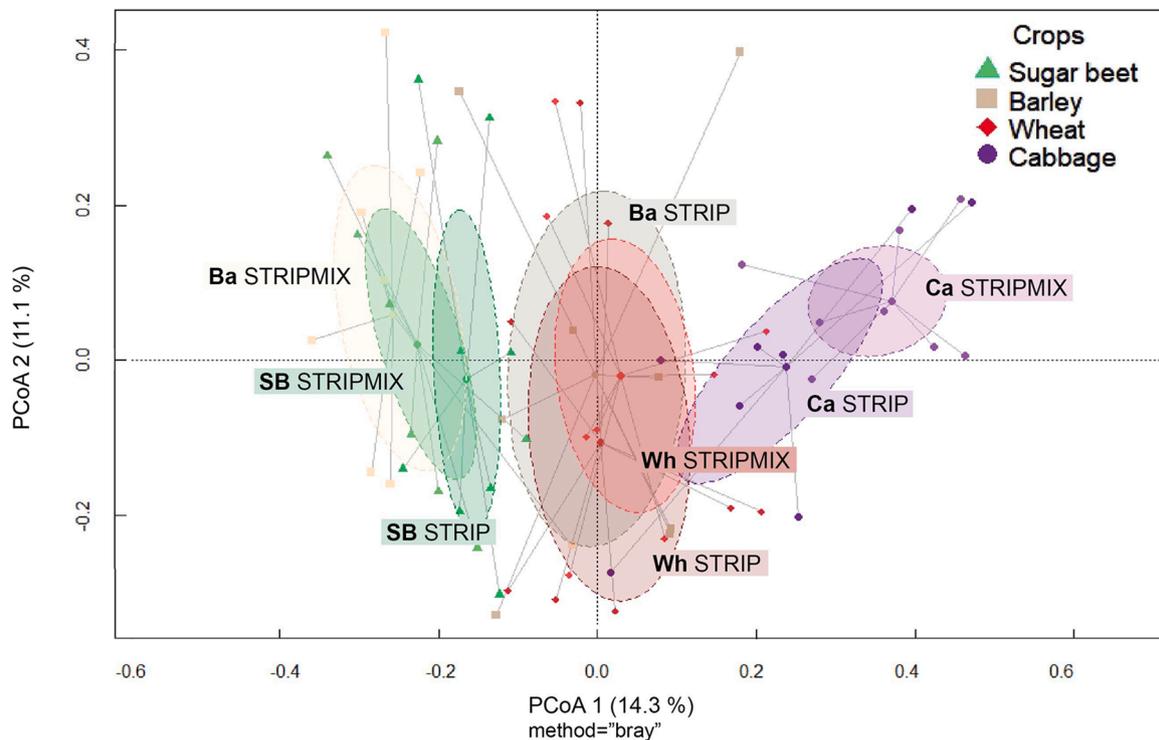


Fig. 4. Principal Coordinate Analysis (PCoA) applied to the Bray-Curtis (BC) distance matrix of aerial arthropod communities in strip cropping fields (2019) in relation to explanatory variables (crop and treatment). A square root transformation was applied on the BC distance matrix before running the PCoA. PCoA axis 1 and 2 explained 14.3% and 11.1% of the variation, respectively. Each point in the figure represents a distinct aerial arthropod community of a single transect in a crop - treatment combination. Each symbol represents a crop; closed circles indicate cabbage (Ca), closed squares barley (Ba), closed triangles sugar beet (SB), and closed diamond wheat (Wh). The text in the boxes refers to treatment (STRIP and STRIPMIX). Translucent ellipses represent 95% of data coverage from BC dissimilarity distance matrix. Centroids (centering all lines to points from a crop - treatment combination) represent means.

Table 4

Comparison of arthropod community composition between crop, round and treatment (STRIP vs. STRIPMIX) in 2019. Coefficients of determination (R^2), F- and p-values of pairwise comparison (PerMANOVA) of arthropod and plant communities between crop, round and strip cropping treatments are shown. Significance levels were obtained by p-values of tested contrasts resulting from PerMANOVA test; * indicates $p < 0.05$, ** indicates $p < 0.01$, *** indicates $p < 0.001$.

CONTRAST	ARTHROPOD COMMUNITY			PLANT COMMUNITY			
	R^2	F	P	R^2	F	P	P
CROP							
Wheat and cabbage	0.162	8.729	< 0.001 ***	0.172	6.251	< 0.001 ***	< 0.001 ***
Wheat and barley	0.106	5.425	< 0.001 ***	0.140	4.902	0.003 **	0.003 **
Wheat and sugar beet	0.137	7.284	< 0.001 ***	0.162	5.795	0.002 **	0.002 **
Cabbage and barley	0.202	11.406	< 0.001 ***	0.136	4.739	0.002 **	0.002 **
Cabbage and sugar beet	0.282	17.637	< 0.001 ***	0.121	4.135	0.005 **	0.005 **
Barley and sugar beet	0.064	3.157	0.003 **	0.135	4.689	0.005 **	0.005 **
Crop effect	0.243	7.143	< 0.001 ***	0.203	8.692	< 0.001 ***	< 0.001 ***
ROUND							
1 and 2	0.084	7.381	< 0.001 ***	0.018	2.339		0.035 *
TREATMENT							
<i>STRIP vs. STRIPMIX</i>							
Wheat	0.063	1.570	0.180	0.324	38.116	< 0.001 ***	< 0.001 ***
Cabbage	0.074	1.399	0.230	0.042	1.055		0.390
Barley	0.140	2.911	0.011 *	0.282	12.953	< 0.001 ***	< 0.001 ***
Sugar beet	0.087	2.005	0.078	0.021	0.657		0.587
Treatment effect	0.016	1.406	0.170	0.036	4.689	< 0.001 ***	< 0.001 ***

neighboring barley strips, and vice versa. This observation underlines the need to consider interactions between specific crop pairs, as apparent effects of strip cropping become visible in some, but not all crop combinations.

4.3. Limitations and implications for future research

The monoculture cabbage reference field (MONO) in our study was 0.24 ha in 2019, which was the maximal attainable experimental field

size, but may still be considered as relatively small as compared to commercial fields. Therefore, we also sampled arthropods in a neighbouring 3.1 ha commercial cabbage monoculture in 2019. The neighbouring field was managed organically but had been planted with a different cabbage cultivar than the experimental fields, and had been sprayed with *Bacillus thuringiensis* (Bt) prior to arthropod sampling. We found 32 *P. xylostella* adults/150 m² in the commercial cabbage monoculture (3.1 ha) compared to 22 adults/150 m² in the MONO reference field (data not presented). This result suggests that the decrease in

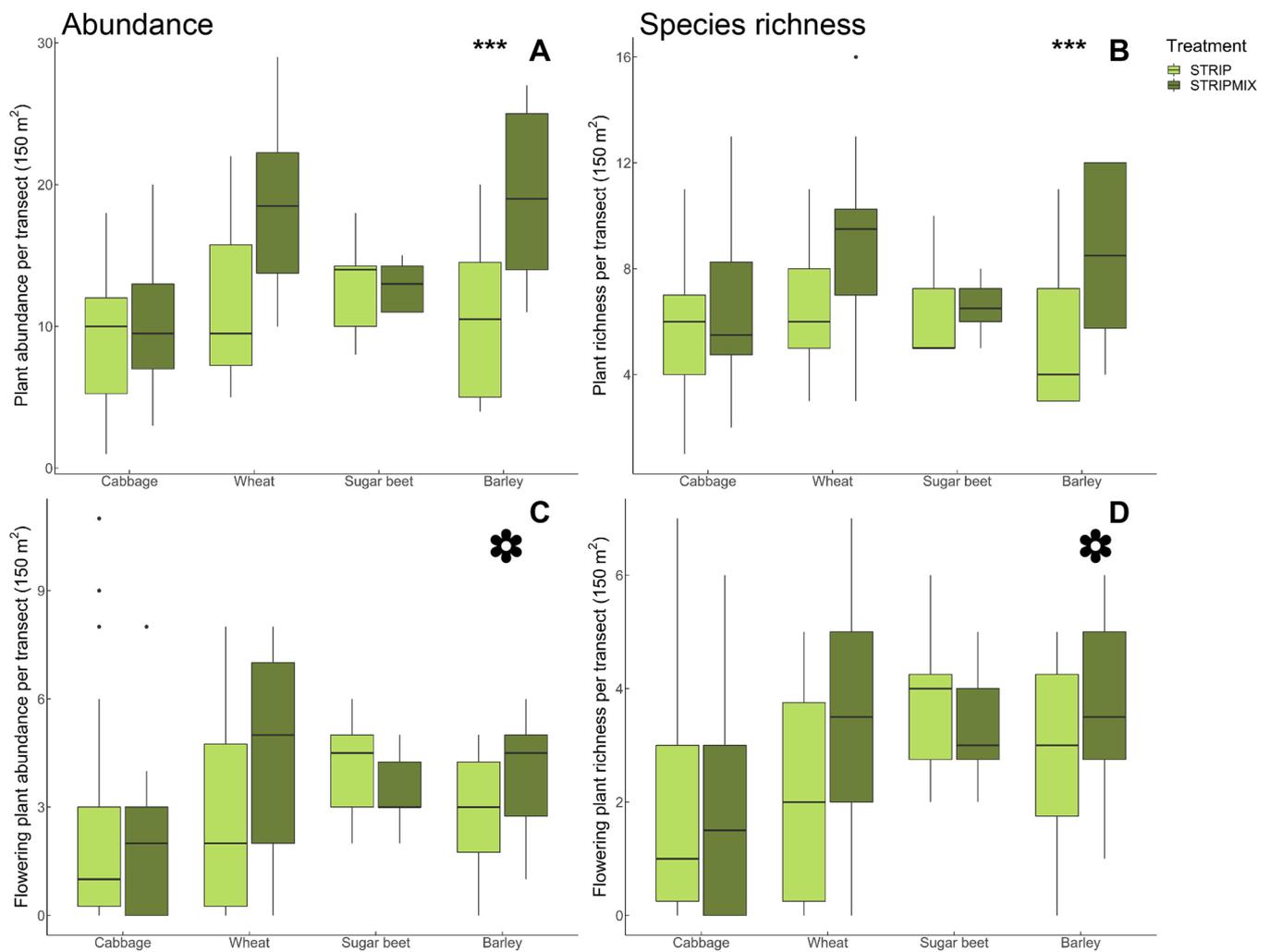


Fig. 5. Abundance and species richness of (flowering) plant communities. Left panels (A-C): plant abundance (A) and flowering plant abundance (C). Right panels (B-D): plant species richness (B) and flowering plant species richness (D). Boxplots indicate data of vegetation in cabbage, wheat, sugar beet and barley for two different strip cropping treatments: cabbage strips alternated with wheat strips and sugar beet strips alternated with barley strips (*STRIP*), and cabbage strips alternated with wheat/faba bean/flower mixture strips and sugar beet strips alternated with barley/pea/flower mixture strips (*STRIPMIX*). Plant abundance and richness data include counts of additional sown plant species and spontaneously established plant species (weeds). Boxplots show plant counts per vegetation plot (150 m²) of two sampling rounds in 2019. Asterisks indicate significance levels of treatments: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Species list: [Supplementary materials Table S.2.1](#).

P. xylostella in *STRIP* compared to *MONO* was conservative when compared to a cabbage monoculture of commercial dimensions (3.1 ha vs. 0.24 ha), and which was treated with biopesticides. Therefore, experiments conducted in commercially sized arable fields may reveal more relevant insights on arthropod responses than small-scale experiments, even though this may be difficult to organize.

5. Conclusions

In this study we explored the effects of field-level configurational and compositional crop heterogeneity on aerial arthropod and plant abundance, species richness and community composition. We show that configurational crop heterogeneity by strip cropping can be effective in reducing herbivore densities and increasing natural enemy richness in cabbage. This makes strip cropping a feasible option to strengthen natural pest suppression (Bianchi, 2022), reducing pesticide use (Thomine et al., 2022; van der Werf and Bianchi, 2022) and to reduce the damage of the major cabbage pest *P. xylostella* (Zalucki et al., 2012). Compositional crop heterogeneity by additional plant species sown in strips increased total aerial arthropod abundance and species richness. Sowing additional crop and non-crop plant species into crops could be a feasible

option to further explore in designing nature-positive cropping systems (Carof et al., 2022). Our results show how configurational and compositional crop heterogeneity are complementary, in terms of reducing pest suppression and increasing farmland arthropod biodiversity. With this, our work contributes to the development and understanding of within-field crop diversification strategies, which can inform the redesign of more biodiversity-friendly cropping systems.

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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.2023.108568](https://doi.org/10.1016/j.agee.2023.108568).

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