Agriculture, Ecosystems and Environment 378 (2025) 109324

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Spatial arrangement of intercropping impacts natural enemy abundance and aphid predation in an intensive farming system

Jennifer B. Thompson [a,b,*], Thomas F. Döring [c], Sonoko Dorothea Bellingrath-Kimura [a,b], Kathrin Grahmann [a], Michael Glemnitz [a], Moritz Reckling [a,d]

[a] *Leibniz Centre for Agricultural Landscape Research (ZALF), Müncheberg 15374, Germany*
[b] *Faculty of Life Science, Thaer-Institute of Agricultural and Horticultural Science, Humboldt-University of Berlin, Berlin 14195, Germany*
[c] *Institute of Crop Science and Resource Conservation, Agroecology and Organic Farming, University of Bonn, 53121, Bonn, Germany*
[d] *Department of Crop Production Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden*

ARTICLE INFO

Keywords:
Carabids
Spiders
Pesticide reduction
Crop diversification
IPM

ABSTRACT

Crop diversification is an increasingly recognized management strategy to support biodiversity and ecosystem services, like pest and disease control, in agricultural systems. However, a significant obstacle to its adoption is the potential trade-off between ecosystem services and optimizing yields. We used a two year, on-farm study in Eastern Germany to test how different spatial arrangements of soy (*Glycine max* L.) and winter wheat (*Triticum aestivum* L.) can affect pest abundance, aphid predation, and natural enemy biodiversity as well as yields. We compared conventional sole cropping to three types of spatially diversified cropping systems: relay intercropping, wide strip cropping, and patch cropping. Strip cropping generally supported some of the highest levels of carabid abundance both years and spider abundance in 2022 without any yield penalties. While the relay system failed due to insufficient precipitation, strip cropping produced similar or higher yields than sole cropping (124 % and 96 % of the sole wheat yield and 96 % and 109 % of sole soy yield in 2022 and 2023, respectively). Strip cropping supported significantly more carabid beetles compared to sole cropped soy both years and sole cropped wheat in 2022. We found significantly different carabid community composition between wheat strips and patches and the corresponding soy strips and patches. There were no differences in aphid abundance between systems. Nevertheless, we found 51 % and 36 % higher aphid predation rates in wheat strips compared to wheat patches in 2022 and 2023. Our results provide initial insights into the potential of strip cropping to support both natural enemies and yields while also being an approachable diversification strategy for farmers.

1. Introduction

Agricultural intensification through chemical input dependence, homogeneous large scale fields, and landscape simplification has led to both increased pest pressure (Gagic et al., 2015; Ziesche et al., 2023) and an overall decrease in non-pest insects (Wagner et al., 2021; Ziesche et al., 2023). It is estimated that pests and pathogens cause 17–30 % of global yield loss in the five most important crops (wheat, rice, maize, soy, and potato) (Savary et al., 2019) and that pest crop damage will increase from climate change (Deutsch et al., 2018), which may increase insecticide usage. This scenario runs counter to the objectives set by EU legislation, including the Farm to Fork strategy and the Regulation on the Sustainable Use of Plant Protection Products. The former aims for 25 % of agricultural land to be under organic farming by 2030, while the latter strives to reduce chemical pesticides by 50 % by 2030, mandating integrated pest management (IPM) practices for all farmers. To attain these ambitious goals, transformative changes supporting better self-regulation of pests on farmland will be imperative.

Cropping system diversification, which includes both spatially and temporally increasing non-crop and crop diversity at the field to landscape level, has been shown to have many benefits for farmers including pest control (Kremen et al., 2012; Tamburini et al., 2020). Increasing temporal crop diversity is linked to reduced pesticide usage (Guinet et al., 2023) as increased rotational diversity or the inclusion of specific crops resistant to pests may decrease pest abundance (Brust and King, 1994). Increased spatial diversity, e.g. from polyculture or intercropping, has also shown stronger pest control benefits than less diverse, sole cropped systems (Beillouin et al., 2021; Chaplin-Kramer and Kremen,

---

[*] Correspondence to: Leibniz Centre for Agricultural Landscape Research (ZALF), Eberswalder Straße 84, Müncheberg 15374, Germany.
E-mail address: jennifer.thompson@zalf.de (J.B. Thompson).

https://doi.org/10.1016/j.agee.2024.109324
Received 11 June 2024; Received in revised form 3 October 2024; Accepted 7 October 2024

2012; Letourneau et al., 2011; Lopes et al., 2016). Spatial crop diversification can control pests through different ecological mechanisms. First, increasing plant diversity can disrupt pest host-finding as pests may not easily locate hosts among non-hosts (Döring and Röhrig, 2016) and must travel farther and more often to find resources, leading to a lower overall density of pests (Barnes et al., 2020; Root, 1973). Secondly, higher plant diversity creates new habitats and resources, both spatially and temporally. These additional resource niches can support higher natural enemy abundance or diversity (Ju et al., 2019; Rakotomalala et al., 2023; Sunderland and Samu, 2000) which can then increase pest predation and decrease crop damage (Barnes et al., 2020; Letourneau et al., 2011). Nevertheless, studies investigating benefits of purely cash crop diversity are rarer compared to studies looking at the addition of semi-natural habitats or non-cash crops like hedgerows, floral strips, or cover crops (Jaworski et al., 2023) and implementing ecological knowledge on crop diversity within a productive farming system remains challenging for farmers.

Intercropping is an ancient practice in which more than one crop is grown simultaneously on the same field. Intercropping can involve numerous arrangements and combinations of crops (Li et al., 2020). Strip cropping, managed by regular farm machinery, consists of wide strips of alternating crops where the strip width is determined by the farmers' current machinery and allows for completely separate management for each strip. Relay intercropping involves alternating single or double rows of crops with different seasons and often different phenologies (e.g. a grain and legume), with one crop harvested while the other is still growing, allowing for longer living cover on the field. Again, already established machinery can be used, albeit a harvest combine attachment may be needed depending on the crops. Another spatial arrangement alternative is patch cropping, a type of large-scale polyculture, in which small (e.g. 0.5 ha) fields are mosaiced in a larger field, allowing for crops to be more precisely matched to appropriate soil properties (Donat et al., 2022).

Spatially diversified systems have been shown to have similar or increased yields compared to sole cropping systems (Chen et al., 2021; C. Li et al., 2023; L. Li et al., 2014), but literature on pest control benefits is scarcer - especially in conjunction with yield data. Strip cropping has been shown to reduce pests compared to sole cropping or less diverse systems (Cuperus et al., 2023; Juventia et al., 2021; Labrie et al., 2016; Parajulee and Slosser, 1999) as well as increasing natural enemy abundance (Cuperus et al., 2023). Other studies found mixed effects of strip cropping on natural enemy diversity metrics (Alarcón-Segura et al., 2022; Labrie et al., 2016). There is little research about the ability of relay cropping to control pests (Lamichhane et al., 2023), especially in wheat based systems, with most studies focused on intercropping cotton with wheat (Lopes et al., 2016). While strip cropping was most successful in decreasing pests and supporting predators, relay intercropping also showed potential (Lopes et al., 2016). For patch cropping, being a new alternative for spatial re-arrangement of cropping systems, only a single study on the arrangement exists, but it found higher pest pressure in the patches compared to sole cropped reference fields (Dovydaitis et al., 2023). Due to the much closer proximity of different crops in relay intercropping, we would expect a different microclimate in this system while wide strip and patch cropping would be more similar to sole cropping. Nevertheless, the two latter systems still offer more spatial habitats and possible temporal diversification of habitats (depending on crops) which could offer refuge to beneficial insects.

This study aimed to explore how various spatial field arrangements affect pests and natural enemy communities and whether these systems could be productive, but less pesticide dependent, management strategies for farmers. We investigated three diversified soy-wheat cropping systems with an on-farm trial in eastern Germany. We focused on soy-wheat systems as grain-legume systems are a well-established intercropping combination. In terms of pest control, wheat is a highly productive crop with higher pesticide usage whereas soy, as a new crop in the region, is rarely affected by pests and diseases. While adding a crop that requires few pesticides would already cause a dilution effect, we focused on whether the addition of a crop through various spatial arrangements could also increase pest predation by supporting natural enemies, as habitat patchiness can positively influence predator diversity (Chase et al., 2010). We hypothesized that 1) diversified systems would have higher or equivalent yields compared to sole cropping, 2) spatially diversified systems would have fewer pests due to the dilution of sole crops, 3) spatially diversified systems would enhance the diversity and abundance of natural enemies and change community composition, 4) leading to greater pest predation in spatially diversified systems.

2. Materials and methods

2.1. Experimental design

The on-farm experiment was located 45 km east of Berlin in Tempelberg, Germany on a large commercial farm typical of the region (52.449391, 14.152694). We studied four different cropping systems: strip intercropping, relay intercropping, patch cropping, and sole cropping over two cropping seasons (2021–2022 and 2022–2023). Strip and relay cropping were arranged in 12 m x 180 m or 24 m x 180 m long strips within a 20–35 ha wheat field (Figs. 1 and 2). The farm established and managed several strips and three were monitored as replicates for each system. Strips were surrounded by the alternative crop on both sides. The variation of strip width was due to the permanent machinery tracks within the field and reflected realistic cropping set-ups for farmers. In the relay treatment, the farmer cultivated 12.5 cm double rows of winter wheat with a double row gap (37.5 cm) for the soy with the exception of the rows where the wheels of the combine harvester pass which came to 56 rows of wheat per 12 m of relay cropping. The wheat field served as a sole cropping reference and the sampling points for this cropping system were more than 200 m away from any diversified cropping system (strips and patches). The soy reference was in a nearby (<2 km) field. Patches of soy and wheat were part of the nearby (<1.5 km) patchCROP experiment (see SM1 for map). Patch cropping consists of smaller field units (72 ×72 m) chosen to select the best crop for the patch soil type which were created applying an advanced cluster analysis for site-specific crop selection (Donat et al., 2022). For that, soil heterogeneity and yield maps at the field scale were analyzed and different crop rotations were developed to fit soil conditions for high and low yielding zones of the field. For the current study, three wheat and three soybean patches (under different sub-management as part of the patchCROP experimental setup) of the "high potential" crop rotation (oilseed rape, winter barley, cover crops, soybean, cover crops, maize, winter wheat) were used for data collection. The different patch sub-management was already established in the patchCROP experiment and includes conventional management, reduced input management, and reduced input management with an adjacent perennial floral strip (Table 1). As the variation in management between the patches could affect results, we first analyzed patches separately to make sure there was no significant effect of patch management on indicators before proceeding with analyses (see 2.6. Statistical Analysis).

While there were at least three replicates per treatment (i.e. three strips, three patches, and three zones within a reference field), each cropping system was located on only one field per year. Crops in all systems were managed conventionally, with occasional mechanical weeding in some patches (Table 1), but no insecticides were applied before or during any monitoring periods. Wheat and soy varieties were recommended from regional variety testing to be high yielding and resistant to disease.

2.2. Monitoring of carabid beetles and spiders

We established 6 sampling points per treatment (2 per system replicate, e.g. 2 per patch or 2 per strip) to monitor pest and natural

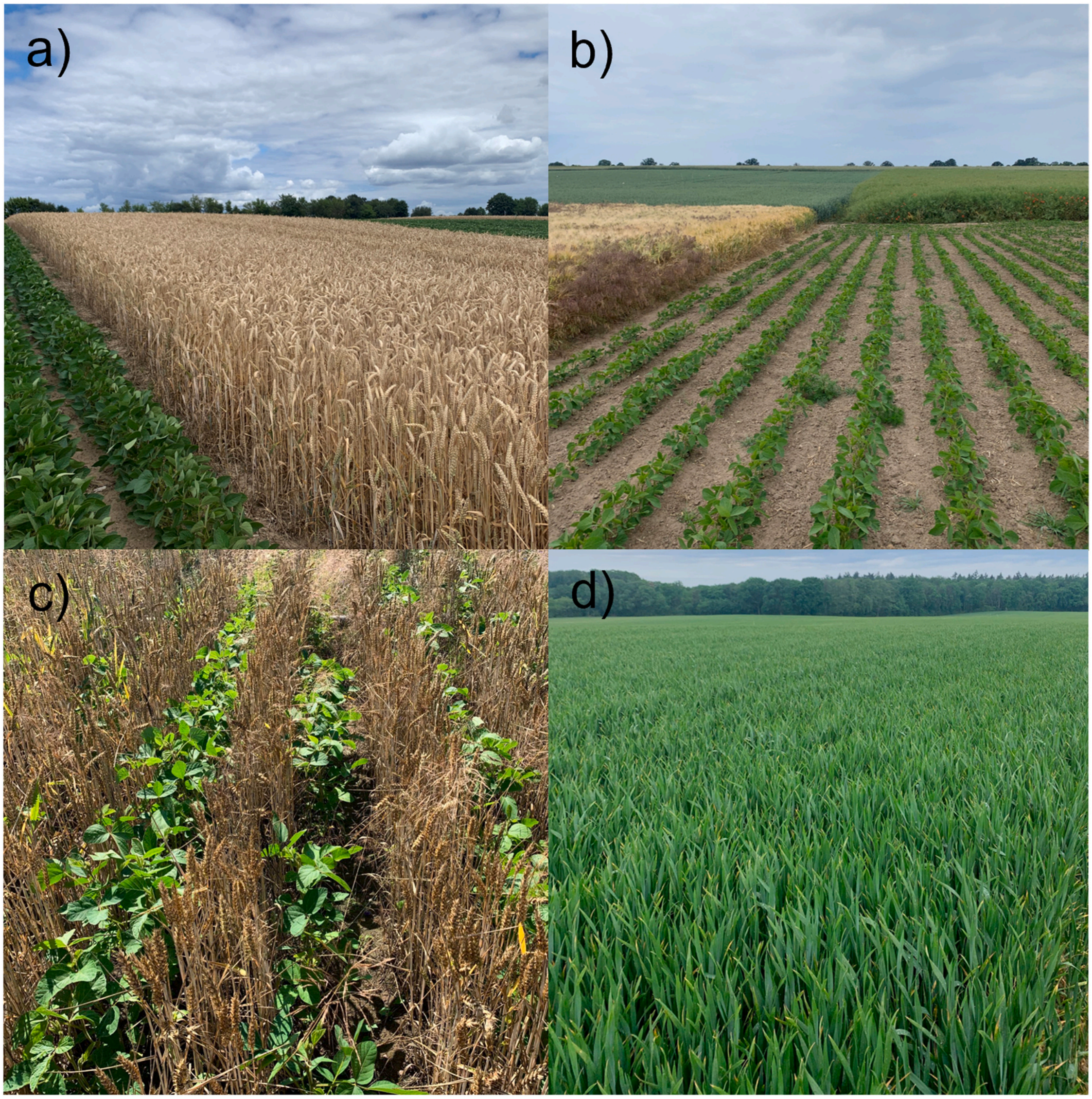

Fig. 1. The cropping system treatments studied on-farm including a) wide strip cropping, b) patch cropping, c) relay cropping, and d) sole cropping of wheat.

enemy (carabid and spider) abundance and diversity (Fig. 2). All sampling points were staggered 20 m apart from each other within treatments and at least 30 m away from traps in other treatments (i.e. traps in soy and wheat strips) to allow approximate independence between traps (Digweed et al., 1995; Ward et al., 2001). Sampling points were at least 50 m away from any field edge. Due to the shape and size of the patches, which were smaller than the other treatments, we established 2 sampling points in each patch, ~ 25 m away from each other. Pitfall traps were installed at each sampling point to collect ground dwelling carabid beetles and spiders. We buried 11 cm high glass jars with a 7.5 cm diameter flush into the soil and filled them with approximately 300 ml of 40 % propylene glycol as a preservation agent (Magagnoli et al., 2018). Jars were open for 14 days in May (May 19th-June 2nd 2022 and May 16th-30th 2023) and June (June 21st-July 5th 2022 and June 13th-27th 2023). All insects in the jar were collected, transferred to 70 % ethanol, and refrigerated until subsequent sample identification. Carabid beetles and spiders were identified to species level using the taxonomy of Müller-Motzfeld (2004) for identification by expert taxonomists (see acknowledgements).

2.3. *Pest monitoring*

Crop pests were monitored at wheat BBCH 75 (milk ripeness) / soy BBCH 13 which corresponded approximately with the June pitfall trap openings. Five plants were randomly selected and inspected for pests every 4 m along a 20 m transect starting from each pitfall trap for a total of 150 plants per treatment. Plants were inspected fully and pests were identified and counted. In the relay cropping treatment only wheat plants were inspected as the soy was barely emerging at this time.

2.4. *Aphid predation rates*

Pest predation was measured with aphid pest predation cards (Boetzl et al., 2020) at approximately wheat BBCH 49 in May, wheat 75 BBCH in June at the beginning of the pitfall trap collection, and wheat BBCH 89 at the start of July after the pitfall traps were closed. We folded 5 ×7 cm green cardstock cards and glued 6 live grain aphids (*Sitobion avenae*) with a non-solvent odorless wood glue (Tortosa et al., 2022). Aphids were in the instar stage and purchased from re-natur GmbH (Ruhwinkel, Germany). Cards were then frozen for at least 24 hours, but no more than 4 days, before being used. Cards were hung with wire at the first flag leaf in wheat. As the soy had just emerged in May, cards in soy

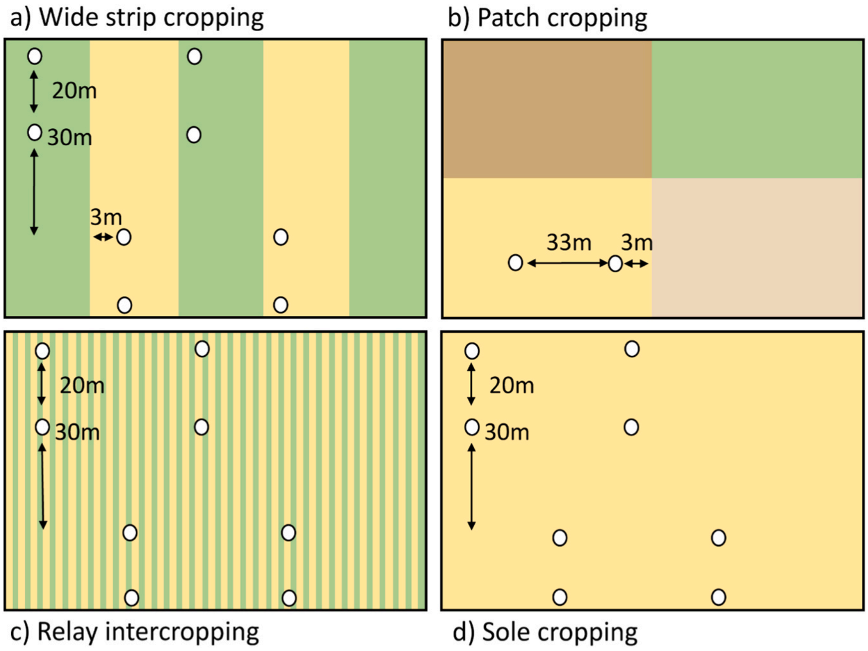

Fig. 2. Sampling design for pitfall traps, pest monitoring, and aphid predation measurements. White circles represent pitfall traps. In a), c), and d) all traps were 20 m away from field edges. Due to approximate scaling of the patches b) depicts where patches meet but does not show the entirety of all patches.

treatments were placed near the ground on sticks to match the height of the emerging crop. In subsequent monitoring, the cards were hung on the first soy leaf node. Cards in relay plots were hung on wheat. Two cards were placed at every pitfall trap for a total of 144 aphids per treatment per time point. Cards were collected after 24 hours in the field and the number of aphids predated was recorded.

2.5. Yield determination

Crop grain yield was measured harvesting 10 m x 2 m replicates in each cropping system using an experimental combine harvester. Harvest replicates were taken approximately at the location of pitfall traps. Five samples were taken in each treatment replicate in the strips, relay, and reference treatments for a total of 15 replicates per treatment while each patch had six replicates for a total of 18 replicated per patch treatment (soy or wheat patch). All wheat treatments and all soy treatments were harvested in the same day (Table 1). Grain was cleaned and corrected to 86 % dry weight for both winter wheat and soybean.

2.6. Statistical analysis

Crop yield was analyzed with linear mixed models with cropping system and year as fixed effects and the soil rating as a random effect with the R package *lmer4*. As each patch did have different management (Dovydaitis et al., 2023), we used an initial model to see if yields and natural enemy abundance varied between patch sub-management types. We found no effect of patch type (i.e. conventional vs. reduced) on soy yield ($p=0.881$) or wheat yield ($p=0.067$) nor on natural enemy abundance. Each patch was then treated as one replicate for the overall patch system in subsequent models to allow a balanced statistical analysis with 3 replicates for all systems. Residuals versus fitted values and normal quantile–quantile (QQ) plots were used as model diagnostics to assess normality of residuals and homogeneity of variance. Tukey HSD post-hoc tests were used to determine variable level differences on statistically significant variables ($p<0.05$) with the *emmeans* package. Data was square root or log transformed if needed to meet model assumptions. To estimate revenues of each cropping system, we assumed a 50 / 50 split of land for each crop in each system and calculated revenues as the yield multiplied by the crop selling price. Prices were obtained by the farmers from their actual selling prices in 2023.

Pest and natural enemy abundances were analyzed with a generalized linear mixed model (GLMM) with a negative binomial distribution with the package *lme4* (Alarcón-Segura et al., 2022). Abundances were measured in two ways, first looking at the difference in cropping system (patch, strip, relay, sole wheat, or sole soy) and then secondly looking at the effects of cropping treatment (soy strip, wheat strip, relay, soy patch, wheat patch, sole soy, or sole wheat). For both spider and carabid abundance we set cropping system or cropping treatment and month as fixed effects and the treatment replicate as a random effect to account for resampling and spatial heterogeneity (including soil rating and distance to natural vegetation). Each year was run separately due to model complexity. Model overdispersion was checked and model fit was assessed with diagnostic plots from the *DHarma* package. For the pest model we set the cropping system and year as fixed effects with the treatment replicate as a random effect.

We analyzed differences in average aphid predation rates between cropping treatments and years with a two-way ANOVA. Wheat and soy systems were analyzed separately due to differences in crop height, and thus trap height that could affect predation rates (Boetzl et al., 2020). To assess differences in species numbers between treatments we calculated actual species richness (R), Pielou species evenness (E), and bias corrected species richness with the Chao1 estimator (Chao, 1984) using the *vegan* package according to the formula:

$$chao1 \quad = \quad Species_{obs} + \frac{Species_S * \quad (Species_S - 1)}{(2 * (Species_D + 1)}$$

Where $Species_S$ and $Species_D$ the number of species with single or double observations. To assess differences in carabid and spider communities between cropping systems and years, we used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices of species abundance data. We tested the significance of species abundance differences between communities with an ANOSIM analysis. All analyses were done in R (R Core Team, 2023, version 4.3.0).

Table 1
Management of the cropping systems.

Sole wheat, strip wheat, patch wheat	Soy-wheat relay intercropping	Sole soy, strip soy, patch soy
Tillage		
Tillage in the fall with disc cultivator, and seedbed preparation	Same as sole wheat	Sole strips: Same as sole wheat All others: Tillage in spring with cultivator, rotary harrow, and seedbed preparation.
Fertilization		
November Micronutrient fertilization (Epsom salt, innofert copper chelate, manganese sulphate, boron) **March** N fertilizer 2022: 323 kg/ha, 2023: 256 kg/ha (urea, NO_3, NH_4 blend). **2023** sole wheat fertilized with additional 85 kg/ja urea treatment **April** N fertilizer 2022: 180 kg/ha, 2023: 296 kg/ha (urea, NO_3, NH_4 blend). **May 2022 only** N fertilizer 225 kg/ha (urea, NO_3, NH_4 blend).	**November** Micronutrient fertilization (Epsom salt, innofert copper chelate, manganese sulphate, boron) **March** N fertilizer 2022: 323 kg/ha, 2023: 256 kg/ha (urea, NO_3, NH_4 blend).	None
	Weed management	
October Post emergence herbicide	**October** Post emergence herbicide	**April 2022** Total herbicide before sowing **May** Pre-emergence herbicide and post-emerge only in June 2023 Two lower input patches received only mechanical weed control in June 2022 and 2023
Fungicides		
May 2022 and 2023 Two lower input patches received less fungicide in 2022, none in 2023	None	None
Sowing		
28.09.21 26.09.22	Same as sole crops	10.05.22 11.05.23
Varieties		
Universum in the patches and Depot (2022) and Asory (2023) in all other treatments	Same as sole crops	Acardia
Harvest		
20.07.22 14.08.23	Same as sole wheat No soy harvest	11.10.22 28.09.23

3. Results

3.1. Crop yield and management

Wheat yields were significantly different between cropping systems ($p<0.0001$, Fig. 3) and there was a significant interaction between year and treatment on yield ($p<0.0001$). Wheat in the relay intercropping treatment yielded 66 % of the sole wheat yield on 58 % of land but the relay soy crop failed both years due to insufficient rainfall. All wheat treatments had significantly higher yields than relay cropping (when not adjusting for the fewer wheat rows) both years with the exception of wheat patches in 2023. In 2022, the wheat strip yield was 21 % higher than wheat reference ($p=0.01$). In 2023, the wheat strip yield was 16 % higher than the patches ($p=0.048$) and the wheat patch yield was 20 % lower than the wheat reference ($p=0.0002$).

Soy yields were significantly higher in 2023 than 2022 ($p<0.0001$) and we found significant treatment effects ($p<0.0001$) as well as a significant interaction between treatment and year ($p=0.04$). The soy strips had a 28 % higher yield than the soy patches in 2022 ($p=0.0003$) and a 13 % higher yield in 2023 ($p=0.033$). The soy patches also had 32 % lower yield than the soy reference in 2022 ($p=0.0006$). Revenue was highest in strip cropping (1450 €/ha), followed by sole cropping (1345 €/ha), patch cropping (1205 €/ha), and relay intercropping (934 €/ha) based on the prices provided by the farmers: 420 €/t for soy and 200 €/t for winter wheat.

3.2. Carabid beetle and spider abundance

We collected 3857 carabid beetles in 2022 and 3849 in 2023. June had significantly higher beetle activity than May both years ($p=0.0007$ and $p<0.0001$ for 2022 and 2023, respectively; Fig. 4) and there was a significant effect of the system (strip, patch, relay, or sole cropping) on carabid abundance both years (2022, $p=0.004$ and 2021, $p<0.0001$). The strip system, averaged over wheat and soy, had more carabids than the soy reference both years ($p=0.04$ and $p<0.0001$) and wheat reference ($p=0.019$) in 2022. Strips also had higher carabid abundance than the relay system ($p=0.025$) in 2022 as well as the patches in 2023 ($p<0.0001$). We found higher beetle abundance in the wheat reference compared to the patches ($p<0.0001$) and relay ($p<0.0001$) in 2023 but there was no difference compared to the strips. The patch system included additional crops compared to the other systems, which could hypothetically pull natural enemies away from the indicator patches (soy and wheat) used in this experiment. However, we found that this was not necessarily the case as in, for example, June 2022, there were on average 51 carabids per trap in winter wheat, soy 30, spring oats 23, winter rye 14.5, winter oilseed rape 170, sunflower 24, winter barley 20, maize 39, and narrow-leafed lupine 44, with an average of 46 carabid beetles per trap (unpublished data) which was lower than our winter wheat patches.

When analyzing cropping treatments separately, carabid abundance was significantly affected by both month ($p<0.0001$, Fig. 4) and treatment in 2022 ($p<0.0001$, Fig. 4) and 2023 ($p<0.0001$ for both). When comparing wheat cropping treatments, the wheat strip had higher carabid abundance than the wheat patches both years ($p=0.049$ and $p=0.0015$) as well as the relay in 2022 ($p=0.0064$). In 2022, there was higher carabid abundance in the wheat patches ($p=0.0487$) than the wheat reference. In 2023, the wheat reference had significantly more carabid beetles than the wheat patches ($p<0.0001$) and relay ($p=0.003$) but not the wheat strip. Soy strips had significantly more carbids than the soy patches both years ($p=0.0078$ and $p<0.0001$) and the soy reference in 2023 ($p<0.0001$).

We collected 3810 spiders in 2022 and 912 in 2023. When analyzing the overall cropping systems, we found significantly more spiders in June than May in 2022 ($p<0.0001$; Fig. 5) and a significant effect of the system on spider abundance per trap in 2022 ($p=0.01$) and 2023 ($p=0.002$). Strips had significantly more spiders than the patches in 2022 ($p=0.014$). In 2023, there were significantly more spiders in the patches ($p=0.005$), wheat reference ($p=0.028$) and relay ($p=0.002$) than the soy reference system.

When looking at individual cropping treatments, in 2022, there were significant effects of treatment both years ($p<0.0001$ both years) and month in 2023 ($p<0.0001$) on spider abundance. In 2022, significantly more spiders were collected in the wheat strips than the wheat patches ($p=0.0005$) and relay ($p=0.0226$). The soy strips had more spiders than the soy reference ($p=0.0386$) and soy patches ($p<0.0001$). In 2023, there was a significant effect of treatment ($p<0.0001$) on spider abundance, but treatment differences were primarily between crops rather than differences in arrangement.

3.3. Species richness and composition

Actual carabid species richness and the Chao1 estimator was highest in relay intercropping followed by the soy strips in 2022 (Table 2). In 2023, actual species richness was very similar between all treatments

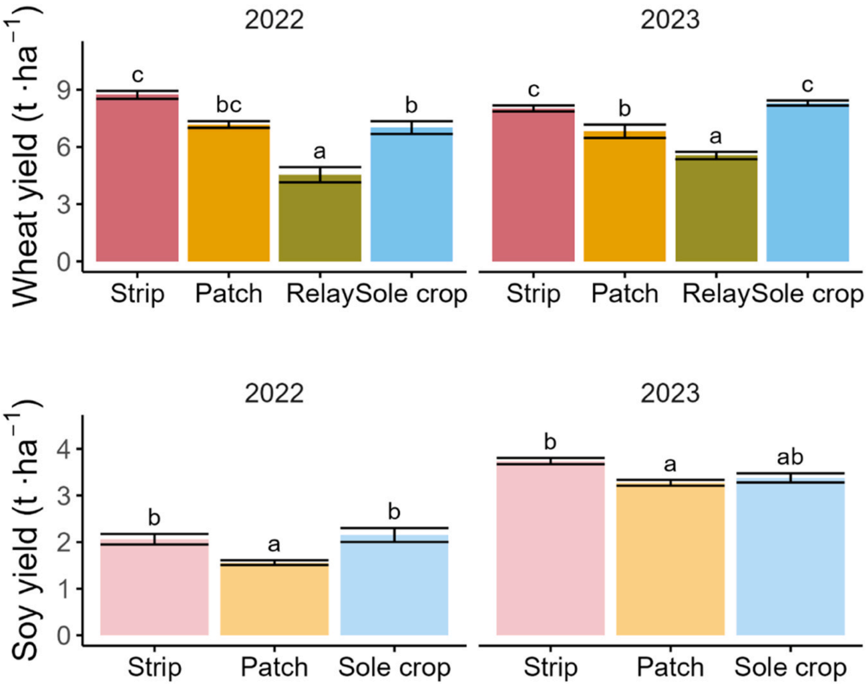

Fig. 3. Winter wheat and soy grain yield of each cropping system in 2022 and 2023. The relay soy system failed due to low precipitation and no yield was harvested. Error bars show standard error.

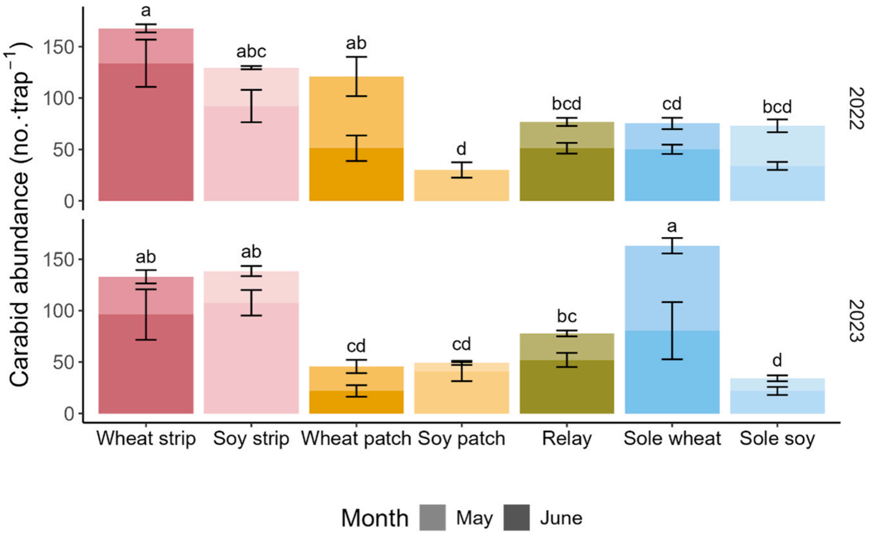

Fig. 4. Average carabid beetle abundance per trap in each cropping treatment. Error bars represent SE. Significance letters refer to comparisons of overall treatment effects, not the effect of month.

(25–28 species) but Chao1 was again highest in relay indicating the presence of more rare species in this treatment. *Poecilus cupreus,* a large carnivorous beetle, was the most abundant beetle in pitfall traps (33 % of all carabids collected), followed by *Calathus fuscipes* (10 %), and *Bembidion lampros* (7 %). We collected three species of endangered carabids in our experiment (Table S2) and all three species were only found in diversified treatments.

The spider Chao1 estimator was much higher in 2022 in sole soy compared to any other treatment. In 2022, both patch treatments had the lowest Chao1 values and much higher species evenness than other treatments. In 2023, the highest species richness and Chao1 were found in the wheat patch and relay treatments. There was no difference in the amount of spiders per hunting strategy (web weavers or active hunters) between treatments. The most common spider species were *Oedothorax apicatus* (50 %), *Phalangium opilio* (10 %), and *Pardosa agrestis* (10 %).

Based on NMDS analysis of carabid and spider communities we identified clusters of species composition and abundance in each treatment (Fig. 6). We found significant clustering of carabid species in 2022 (anosim R=0.723, p<0.0001, stress=0.15) and 2023 (asonim R=0.584, p<0.0001, stress=0.12). We also found significant clustering of spider composition and abundance in 2022 (anosim R=0.552, p<0.0001, stress=0.09) and 2023 (asonim R=0.473, p<0.0001, stress=0.19). Notably, for carabids both years and spiders in 2022, we found similar but separate clusters for communities in wheat and soy strips and even larger distances between soy and wheat patches. For carabids, all wheat treatments tended to separate from all soy treatments, with the soy strip being closest to the wheat treatments.

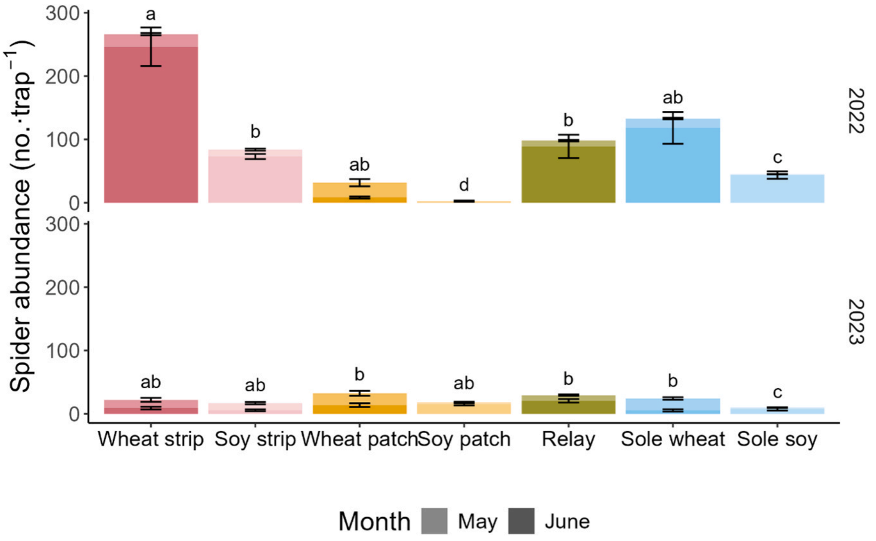

Fig. 5. Average spider abundance per trap in each treatment. Error bars represent SE. Significance letters refer to comparisons of overall treatment effects, not the effect of month.

Table 2
Carabid beetle and spider species richness (R), estimated richness (Chao1) and Pielou evenness (E).

	Carabids 2022			Carabids 2023			Spiders 2022			Spiders 2023		
	R	Chao1	E	R	Chao1	E	R	Chao1	E	R	Chao1	E
Sole wheat	25	31±5	0.78	27	29±3	0.58	32	45±10	0.47	19	23±4	0.75
Sole soy	23	25±3	0.67	28	30±3	0.83	16	61±30	0.43	15	36±17	0.79
Wheat strip	23	24±2	0.66	25	26 ±1	0.65	29	43±11	0.40	20	24±4	0.72
Soy strip	21[a]	42±17	0.60	27	28±1	0.65	18[a]	27±9	0.54	15	36±17	0.78
Relay	30	48±15	0.70	26	37±11	0.75	24	27±3	0.46	29	59±21	0.64
Soy patch	18[b]	21±4	0.79	25	26±2	0.63	7[b]	12±6	0.94	22	35±10	0.62
Wheat Patch	30	31±2	0.65	27	28±1	0.65	17	20±4	0.78	27	66±30	0.76

Treatments had 12 traps while superscripts [a] and [b] indicate where only 10 and 6 traps were collected, respectively.

3.4. Pests and predation

We counted 481 live aphids and 65 aphid mummies and 97 % of live aphids were found in wheat treatments. We found no effect of treatment on aphid abundance (Fig. S2; $p=0.57$) and the numbers of aphids per 50 plants ranged from 0 to 46. There were significantly more aphids in 2023 than 2022 (Fig S2; $p=0.03$).

Predation was higher in 2023 than 2022 ($p<0.00001$; Fig. 7) and cropping treatment affected the average predation rate in wheat treatments ($p=0.003$) but there was no interaction between wheat treatment and year. There was no effect of year ($p=0.056$) or treatment ($p=0.066$) in soy systems. Wheat strips had higher average predation than the wheat patches ($p=0.001$) and the wheat reference ($p=0.045$). There was no relationship between spider or carabid abundance and predation.

4. Discussion

4.1. Strip cropping supports higher carabid and spider abundance while maintaining sole crop yields

Our study revealed that wide strip intercropping maintained yields as high as or higher than sole cropping as well as supporting some of the highest abundances of natural enemies. Strip cropping always had equivalent or higher abundances of carabid beetles than sole cropping or patch cropping. A wide strip experiment in France (18–36 m soy strips) found similar yield trends between strips and sole crops (Labrie et al., 2016). A meta-analysis of various intercropping management practices found that strip cropping generally increased the abundance of natural enemies with cereal-legume combinations having the strongest effect size (Rakotomalala et al., 2023). Strips were likely able to maintain high yields because they are managed identically to their respective sole crop. They act as narrow fields and thus do not require additional driving and can handle pesticides that mixed crops or relay cropping cannot. Narrow strip or row intercropping has been shown to increase yields or land equivalent ratios compared to sole cropping due to the high yields of margin rows and efficient resource utilization (Chen et al., 2021; C. Li et al., 2023; L. Li et al., 2014). However, this management is difficult to implement with current machinery in European farms. Moreover, the positive effects of niche differentiation (complementarity) might turn into negative effects when it comes to resource competition e.g. for water between crops (Yin et al., 2020) which is nearly completely avoided in wide strip intercropping.

Wide strips may support more natural enemies than patch or sole cropping from increased edge effects. The edge:area ratio (m/ha) was highest in the strip intercropping design e.g. with 1800 m/ha for 12 m x 150 m strips, 966 m/ha for 24 m x 150 m strips, 556 m/ha for patches and 89 m/ha for an average 20 ha square sole cropped field in our region. Activity-density and species richness of spiders (Clough et al., 2005) and carabids (Zhao et al., 2013) have been found to be higher at field edges than centers. High mean field edge:area ratios were also correlated with less aphid establishment and survival (Östman et al., 2001). Edges support arthropods with different traits than field interiors (Gallé et al., 2020) and habitat complexity can support higher abundances of arthropods like spiders (Ávila et al., 2017). Intercropping with a non-legume crop rather than a legume can support more predators and parasitoids (Yousefi et al., 2024), a pattern we saw with the wheat patches and strips compared to the soy treatments. It is possible that the autumn sown wheat strips, which are undisturbed in the spring, can

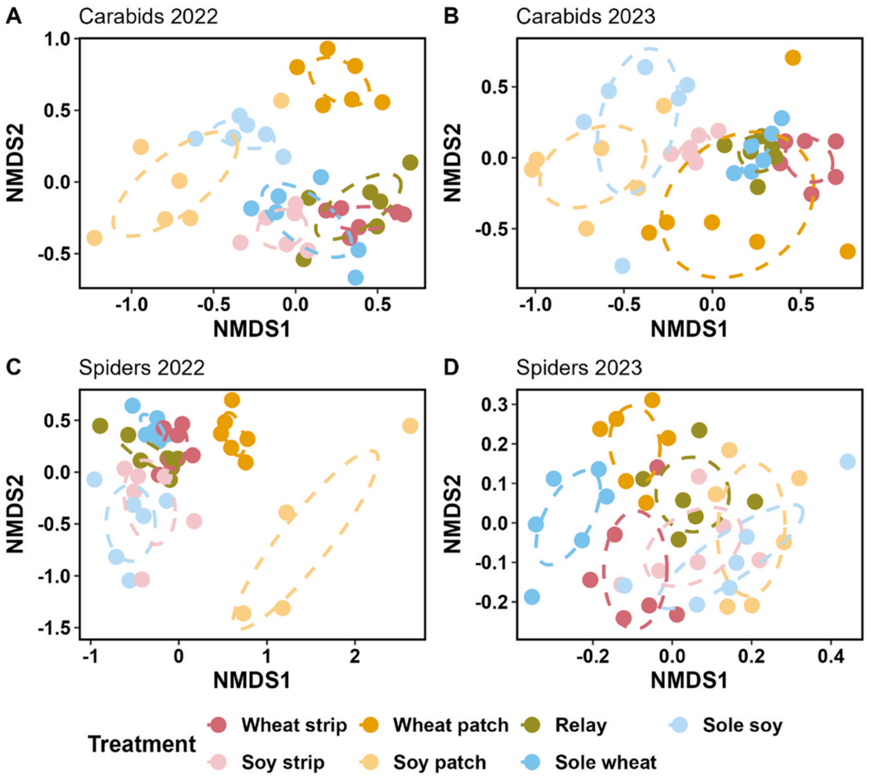

Fig. 6. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity distances of beetle (A and B) and spider (C and D) communities in 2022 (A and C) and 2023 (B and D). Points represent pitfall traps. Ellipses are a standard deviation from the mean.

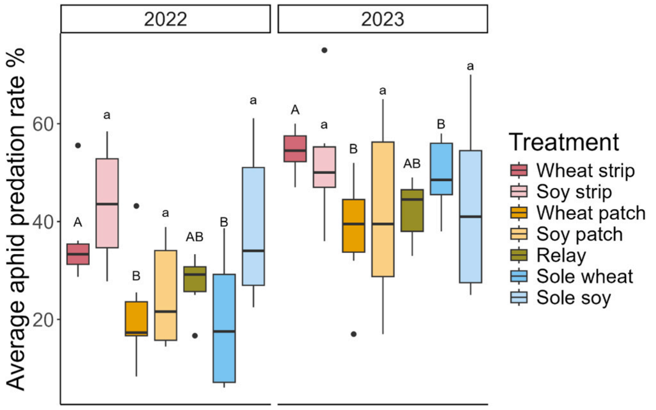

Fig. 7. Aphid predation rates per treatment. Rates are averaged across all predation sampling times. As soy and wheat treatments were analyzed separately, lowercase significance letters are used for soy treatments and uppercase significance letters were used for wheat treatments. Relay cropping was included only in the wheat treatment.

serve as an early reservoir of natural enemies for the spring cultivated soy whereas in a large, conventional soy field, beetles would have to recolonize the field from the field margins. Studies conducted by Alarcón-Segura et al. (2022) and Järvinen et al. (2023) have reported mixed results, with strip cropping supporting only specific groups of natural enemies during certain time periods. It is also worth noting that the effects of wide strip cropping on natural enemy abundance can be variable and might be influenced by crop type and strip width as field interiors are also important habitats for natural enemies (Gallé et al., 2020).

Spider abundance was highly variable between the study years with abundance in 2023 reaching only 24 % of 2022. This is partially attributed to high rainfall in the June 2023 collection period, in accordance with findings from Lensing et al. (2005) who found spider movement limited by precipitation. Pitfall trap catches from 2022 show that spider activity densities were much higher in wheat compared to soy treatments and in strips compared to respective patch or reference treatments. According to Triquet et al. (2022) overwintering cover crop strips hosted a higher activity density of ground beetles and spiders, serving as reservoirs for natural enemies. Overwintering winter wheat strips as found in our experiment, can act as these reservoirs, potentially supporting colonization of the soy strips later in the season. In 2023 no trends could be seen, possibly due to the low activity-density from high precipitation. Outcomes from other studies have shown the effects of intercropping on spider population composition are dependent on crop species combinations and row width management, while the effects on spider abundances were unclear (Alarcón-Segura et al., 2022; Cai et al., 2010; Järvinen et al., 2023).

4.2. Relay and patch cropping are associated with fewer arthropods and lower yields

The relay system was an economic failure as the soy crop died even though the relay wheat had a high yield. There was low soil moisture in the relay system at the time of soy drilling, as the winter wheat had already consumed most of the soil water, and the low precipitation in our region was not enough to overcome this. Moreover, relay intercropping supported only intermediate abundances of natural enemies. Yields in the patches were some of the lowest in our study. Due to the layout of the patches, farmers' large machinery cannot work as usual, e.g. mechanical weeding was more difficult as the patches were not large enough to allow full speed of the tractors. This, combined with the lower herbicide usage in some patches, may have led to the slightly higher weed cover in the patches (Supplemental materials) which can negatively affect yields. The patches had inconsistent outcomes concerning natural enemy abundance but generally had some of the lowest activity-densities per trap. Patch cropping involves interactions with adjacent other crops within the experiment and semi-natural habitats which could affect natural enemy and pest communities. However, out of the 9 crops in the patchCROP rotation in, for example June 2022, wheat patches had the second highest carabid abundance and this abundance was close to the system average catch. This indicates that our soy and wheat indicator patches were representative of the system and that the average number of beetles per trap in the patches is still lower than most of our other treatments. Many natural enemy species have habitat preferences with some preferring edges and others field interiors, thus maintaining a minimum field area may be important to maintain distinct habitat qualities to support both edge and center species (Gallé et al., 2020). Nevertheless, it is difficult to disentangle some of the management versus layout effects on natural enemies in this experiment and further research is needed to identify the limits and potential challenges with more diversified cropping on smaller fields such as patches.

4.3. *Spatial cropping arrangement drives community composition*

Different spatially diversified cropping treatments influenced the community compositions of natural enemies, as revealed by the NMDS analysis. The variations in species preferences and composition between different crops, even adjacent ones like soy and wheat patches and strips, indicate that natural enemy composition was not random but likely driven by preferences for specific crops and spatial designs. In both years, soy and wheat patches show the strongest differentiation in community composition of spiders and carabids, while strip cropping also showed differing community composition, albeit more similar than the patches. This is in line with findings from Hummel et al. (2012), who found carabid species showing differing responses to different crops in intercropping. We found *Pterostichus melanarius*, known to favor complex and taller crops (Busch et al., 2021; Döring and Kromp, 2003), primarily in wheat treatments but not in soy strips, which were bare in the first sampling and still shorter in the second. Conversely, the spring breeder *Bembidion properans* was found more often in soy strips, likely due to its preference for open spaces (Ropek and Jaworska, 1994). Strips and patches offer spatial and temporal diversification, accommodating species with different emergence times and habitat preferences within a single field. For example, wheat is tilled late in the fall and harvested in July, while soy is cultivated in the spring and harvested in autumn which disrupts groups with different emergence times. Järvinen et al. (2023) also reported a strong response in the abundance and species assemblage of carabid beetles in intercropping of fava beans with turnip rape as the season progressed.

Despite clear composition patterns among treatments, species richness results were less consistent. The only consistent response between the two years in our study was that relay cropping supported the highest number of carabid species. A study manipulating the row width of wheat found that wide row wheat, as found in relay intercropping, had more *Lycosidae* spiders than conventional narrow row wheat (Smith and Jones, 2007). More species may prefer the mix of dense (wheat) and bare (gap for soy) plant cover in the relay treatment. Nevertheless, a meta-analysis found that strip cropping did not affect beneficial arthropod species richness (Rakotomalala et al., 2023) and spider species richness may be more affected by non-crop vegetation in the landscape rather than management (Schmidt et al., 2005) as spiders need to recolonize fields.

4.4. *Pests unaffected by cropping treatment*

We did not find any effect of cropping treatment on pest abundance in the field, contrasting with our initial hypotheses. This is partially likely due to the overall low number of aphids which was far below the threshold for pesticide application. While wheat is known to have several pests in the study region, including aphids and cereal leaf beetle larvae, soy does not have established pests. This may have helped lower the number of aphids which we consider too low to draw any conclusions from. Other studies on intercropping have found that wide strip cropping can reduce or constrain pests (Järvinen et al., 2023; Labrie et al., 2016). However, a three year study comparing rapeseed patches to sole cropped rapeseed found higher pest pressure in the patches, but this did not necessarily translate to yield losses (Dovydaitis et al., 2023). Pest abundance is also affected by many other factors than just plant diversity including the local landscape (Rusch et al., 2013), previous crops in the rotation (Buntin et al., 2007), and overall host plant quality (Martinez et al., 2021). We also found no relationship between spider or carabid abundance and predation rates or pest numbers. Other groups of natural enemies not measured in this study may have contributed to pest control (Järvinen et al., 2023), for example parasitic wasps or ladybirds (Schmidt et al., 2003). We did find, however, that wheat strips had higher average aphid predation rates than wheat patches and sole wheat and other studies of strip cropping also found that it can support increased pest parasitism or predation. Croijmans et al. (2023) found that narrow strips (3 m x 45 m) of wheat and cabbage were the best for supporting parasitism of pests compared to sole cropping and pixel cropping. They hypothesized that there is an 'ideal' amount of biodiversity between supporting natural enemies and not making it too difficult for them to find pests and also recommend strip cropping as the best option for farmers.

4.5. *Limitations and future perspectives*

The study was conducted on a single farm, encompassing multiple fields that changed over the two years of cultivation. While this provides valuable initial insights, future research should include additional fields and farms across a broader landscape to disentangle the effects of the local landscape and field level diversification. Furthermore, the relay intercropping system failed due to the low soil moisture which prevented soy establishment, rendering it unsuitable for comparison due to its lack of agronomic viability in our region. Future studies need to consider different row spacing in cereals (12.5–37.5 cm) or crop combinations (e.g. lupin-rye, rapeseed-barley) to explore the viability of the system within a crop rotation in our region. Nevertheless, this study stands out as one of the first to systematically compare numerous spatial arrangements from both agronomic and ecological perspectives. Challenges for practical implementation include higher complexity of multiple field operations, management of the headland areas (damage of crops due to multiple passes at different time periods), and resulting administrational uncertainties.

5. Conclusions

We found that the spatial arrangement of intercropping impacted natural enemy abundances, aphid predation rates, and the community assemblage of carabids and spiders. Strip intercropping increased agroecological benefits, by supporting higher carabid abundance and aphid predation rates, with no yield penalties to the farmers. This study was one of the first of its kind to compare yields and ecological benefits of wide strip, relay, and patch intercropping with sole cropping in a commercial farming context in central Europe. While some diversified systems were not as productive as sole cropping, the strip cropping results show the potential of the system for farmers to diversify their farms in a manner that involves no additional machinery with direct benefits for biodiversity. Challenges for implementation remain, for example, with the management of the headland areas. Thus, optimal spatial management plans for farmers that balance yields, economic returns, and ecological goals need to be co-designed.

Funding

This project was supported by the Leibniz Centre for Agricultural Landscape Research (ZALF) through the integrated priority project:

Cropping system diversification to increase the resilience of farming systems (divCROP) 2021–2024. KG acknowledges support from BMBF for the Junior Research Group SoilRob, project ID 031B1391.

CRediT authorship contribution statement

Moritz Reckling: Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition. **Michael Glemnitz:** Writing – review & editing, Resources, Methodology. **Kathrin Grahmann:** Writing – review & editing, Resources. **Sonoko Dorothea Bellingrath-Kimura:** Writing – review & editing, Methodology, Conceptualization. **Thomas F. Döring:** Writing – review & editing, Methodology, Conceptualization. **Jennifer B. Thompson:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis.

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.

Acknowledgements

We would like to thank Christoph Müller, Julien Cadiran, and Kritika Chouhan for their support in the field as well as everyone in the working group Provisioning of Biodiversity in Agricultural Systems for their help. We thank Drs. Ingo Brunk and Christoph Muster for their help identifying carabids and spiders. We also are especially appreciative to everyone on the patchCROP team and the project partner farm Komturei Lietzen GmbH who made the experiment possible, and the Julius-Kühn-Institut (JKI). The maintenance of the patchCROP infrastructure is supported by the Leibniz Centre for Agricultural Landscape Research.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109324.

Data Availability

Data will be made available on request.

References

Alarcón-Segura, V., Grass, I., Breustedt, G., Rohlfs, M., Tscharntke, T., 2022. Strip intercropping of wheat and oilseed rape enhances biodiversity and biological pest control in a conventionally managed farm scenario. J. Appl. Ecol. *59* (6), 1513–1523. https://doi.org/10.1111/1365-2664.14161.

Ávila, A.C., Stenert, C., Rodrigues, E.N.L., Maltchik, L., 2017. Habitat structure determines spider diversity in highland ponds. Ecological research 32, 359–367.

Barnes, A.D., Scherber, C., Brose, U., Borer, E.T., Ebeling, A., Gauzens, B., Giling, D.P., Hines, J., Isbell, F., Ristok, C., Tilman, D., Weisser, W.W., Eisenhauer, N., 2020. Biodiversity enhances the multitrophic control of arthropod herbivory. Sci. Adv. *6* (45), eabb6603. https://doi.org/10.1126/sciadv.abb6603.

Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., Makowski, D., 2021. Positive but variable effects of crop diversification on biodiversity and ecosystem services. Glob. Change Biol. *27* (19), 4697–4710. https://doi.org/10.1111/gcb.15747.

Boetzl, F.A., Konle, A., Krauss, J., 2020. Aphid cards – Useful model for assessing predation rates or bias prone nonsense? J. Appl. Entomol. *144* (1–2), 74–80. https://doi.org/10.1111/jen.12692.

Brust, G.E., King, L.R., 1994. Effects of crop rotation and reduced chemical inputs on pests and predators in maize agroecosystems. Agric. Ecosyst. Environ. *48* (1), 77–89. https://doi.org/10.1016/0167-8809(94)90077-9.

Buntin, G.D., Cunfer, B.M., Phillips, D.V., Wilson, J.P., 2007. Sequence and rotation effects on pest incidence and grain yield of double-cropped soybean and pearl millet after winter wheat and Canola. Crop Manag. *6* (1), 1–10. https://doi.org/10.1094/CM-2007-1023-01-RS.

Busch, A.K., Wham, B.E., Tooker, J.F., 2021. Life history, biology, and distribution of Pterostichus melanarius (Coleoptera: Carabidae) in North America. Environ. Entomol. *50* (6), 1257–1266. https://doi.org/10.1093/ee/nvab090.

Cai, H., You, M., Lin, C., 2010. Effects of intercropping systems on community composition and diversity of predatory arthropods in vegetable fields. Acta Ecol. Sin. *30* (4), 190–195. https://doi.org/10.1016/j.chnaes.2010.06.001.

Chao, A., 1984. Non-parametric estimation of the classes in a population. Scand. J. Stat. *11*, 265–270. https://doi.org/10.2307/4615964.

Chaplin-Kramer, R., Kremen, C., 2012. Pest control experiments show benefits of complexity at landscape and local scales. Ecol. Appl. *22* (7), 1936–1948. https://doi.org/10.1890/11-1844.1.

Chase, J.M., Burgett, A.A., Biro, E.G., 2010. Habitat isolation moderates the strength of top-down control in experimental pond food webs. Ecology *91* (3), 637–643. https://doi.org/10.1890/09-0262.1.

Chen, J., Engbersen, N., Stefan, L., Schmid, B., Sun, H., Schöb, C., 2021. Diversity increases yield but reduces harvest index in crop mixtures. Nat. Plants 1–6. https://doi.org/10.1038/s41477-021-00948-4.

Clough, Y., Kruess, A., Kleijn, D., Tscharntke, T., 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. J. Biogeogr. *32* (11), 2007–2014. https://doi.org/10.1111/j.1365-2699.2005.01367.x.

Croijmans, L., van Apeldoorn, D.F., Sanfilippo, F., Zangpo, T., Poelman, E.H., 2023. Crop species diversity levels with attract and reward strategies to enhance Pieris brassicae parasitism rate by Cotesia glomerata in strip intercropping. Funct. Ecol. https://doi.org/10.1111/1365-2435.14502.

Cuperus, F., Ozinga, W.A., Bianchi, F.J.J.A., Croijmans, L., Rossing, W.A.H., van Apeldoorn, D.F., 2023. Effects of field-level strip and mixed cropping on aerial arthropod and arable flora communities. Agric. Ecosyst. Environ. *354*, 108568. https://doi.org/10.1016/j.agee.2023.108568.

Deutsch, C.A., Tewksbury, J.J., Tigchelaar, M., Battisti, D.S., Merrill, S.C., Huey, R.B., Naylor, R.L., 2018. Increase in crop losses to insect pests in a warming climate. Science *361* (6405), 916–919. https://doi.org/10.1126/science.aat3466.

Digweed, S.C., Currie, C.R., Cárcamo, H.A., & Spence, J.R. (1995). Digging Out The" Digging-in Effect" of Pitfall Traps: Influences of Depletion and Disturbance on Catches of Ground Beetles (Coleoptera: Carabidae).

Donat, M., Geistert, J., Grahmann, K., Bloch, R., Bellingrath-Kimura, S.D., 2022. Patch cropping- a new methodological approach to determine new field arrangements that increase the multifunctionality of agricultural landscapes. Comput. Electron. Agric. *197*, 106894. https://doi.org/10.1016/j.compag.2022.106894.

Döring, T.F., Kromp, B., 2003. Which carabid species benefit from organic agriculture?—a review of comparative studies in winter cereals from Germany and Switzerland. Agric. Ecosyst. Environ. *98* (1), 153–161. https://doi.org/10.1016/S0167-8809(03)00077-X.

Döring, T. f, Röhrig, K., 2016. Behavioural response of winged aphids to visual contrasts in the field. Ann. Appl. Biol. *168* (3), 421–434. https://doi.org/10.1111/aab.12273.

Dovydaitis, E., Kunze, T., Born, F., Ewert, F., Dachbrodt-Saaydeh, S., Grahmann, K., 2023. Assessing pollen beetle dynamics in diversified agricultural landscapes with reduced pesticide management strategies: exploring the potential of digital yellow water traps for continuous, high-resolution monitoring in oilseed rape. Article 1. Landbauforsch. J. Sustain. Org. Agric. *72* (1). https://doi.org/10.5073/LBF.2023.01.03.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc. R. Soc. B Biol. Sci. *282* (1801), 20142620. https://doi.org/10.1098/rspb.2014.2620.

Gallé, R., Geppert, C., Földesi, R., Tscharntke, T., Batáry, P., 2020. Arthropod functional traits shaped by landscape-scale field size, local agri-environment schemes and edge effects. Basic Appl. Ecol. *48*, 102–111. https://doi.org/10.1016/j.baae.2020.09.006.

Guinet, M., Adeux, G., Cordeau, S., Courson, E., Nandillon, R., Zhang, Y., Munier-Jolain, N., 2023. Fostering temporal crop diversification to reduce pesticide use. Nat. Commun. *14* (1). https://doi.org/10.1038/s41467-023-43234-x.

Hummel, J.D., Dosdall, L.M., Clayton, G.W., Harker, K.N., O'Donovan, J.T., 2012. Ground beetle (Coleoptera: Carabidae) diversity, activity density, and community structure in a diversified agroecosystem. Environ. Entomol. *41* (1), 72–80. https://doi.org/10.1603/EN11072.

Järvinen, A., Hyvönen, T., Raiskio, S., Himanen, S.J., 2023. Intercropping shifts the balance between generalist arthropod predators and oilseed pests towards natural pest control. Agric., Ecosyst. Environ. *348*, 108415. https://doi.org/10.1016/j.agee.2023.108415.

Jaworski, C.C., Thomine, E., Rusch, A., Lavoir, A.-V., Wang, S., Desneux, N., 2023. Crop diversification to promote arthropod pest management: a review. Agric. Commun. *1* (1), 100004. https://doi.org/10.1016/j.agrcom.2023.100004.

Ju, Q., Ouyang, F., Gu, S., Qiao, F., Yang, Q., Qu, M., Ge, F., 2019. Strip intercropping peanut with maize for peanut aphid biological control and yield enhancement. Agric. Ecosyst. Environ. *286*, 106682. https://doi.org/10.1016/j.agee.2019.106682.

Juventia, S.D., Rossing, W.A.H., Ditzler, L., van Apeldoorn, D.F., 2021. Spatial and genetic crop diversity support ecosystem service delivery: a case of yield and biocontrol in Dutch organic cabbage production. Field Crops Res. *261*, 108015. https://doi.org/10.1016/j.fcr.2020.108015.

Kremen, C., Iles, A., Bacon, C., 2012. Diversified farming systems: an agroecological, systems-based alternative to modern industrial agriculture. Ecol. Soc. *17* (4). https://doi.org/10.5751/ES-05103-170444.

Labrie, G., Estevez, B., Lucas, E., 2016. Impact of large strip cropping system (24 and 48 rows) on soybean aphid during four years in organic soybean. Agric., Ecosyst. Environ. *222*, 249–257. https://doi.org/10.1016/j.agee.2015.11.029.

Lamichhane, J.R., Alletto, L., Cong, W.-F., Dayoub, E., Maury, P., Plaza-Bonilla, D., Reckling, M., Saia, S., Soltani, E., Tison, G., Debaeke, P., 2023. Relay cropping for sustainable intensification of agriculture across temperate regions: Crop management challenges and future research priorities. Field Crops Res. *291*, 108795. https://doi.org/10.1016/j.fcr.2022.108795.

Lensing, J.R., Todd, S., Wise, D.H., 2005. The impact of altered precipitation on spatial stratification and activity-densities of springtails (Collembola) and spiders (Araneae). Ecol. Entomol. *30* (2), 194–200. https://doi.org/10.1111/j.0307-6946.2005.00669.x.

Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutiérrez, C., López, S.D., Mejía, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? a synthetic review. Ecol. Appl. *21* (1), 9–21. https://doi.org/10.1890/09-2026.1.

Li, C., Hoffland, E., Kuyper, T.W., Yu, Y., Zhang, C., Li, H., Zhang, F., van der Werf, W., 2020. Syndromes of production in intercropping impact yield gains. Nat. Plants *6* (6). https://doi.org/10.1038/s41477-020-0680-9.

Li, C., Stomph, T.-J., Makowski, D., Li, H., Zhang, C., Zhang, F., van der Werf, W., 2023. The productive performance of intercropping. Proc. Natl. Acad. Sci. *120* (2), e2201886120. https://doi.org/10.1073/pnas.2201886120.

Li, L., Tilman, D., Lambers, H., Zhang, F.-S., 2014. Plant diversity and overyielding: insights from belowground facilitation of intercropping in agriculture. N. Phytol. *203* (1), 63–69. https://doi.org/10.1111/nph.12778.

Lopes, T., Hatt, S., Xu, Q., Chen, J., Liu, Y., Francis, F., 2016. Wheat (Triticum aestivum L.)-based intercropping systems for biological pest control. Pest Manag. Sci. *72* (12), 2193–2202. https://doi.org/10.1002/ps.4332.

Magagnoli, S., Masetti, A., Depalo, L., Sommaggio, D., Campanelli, G., Leteo, F., Burgio, G., 2018. Cover crop termination techniques affect ground predation within an organic vegetable rotation system: a test with artificial caterpillars. Biol. Control 117, 109–114.

Martinez, D.A., Loening, U.E., Graham, M.C., Gathorne-Hardy, A., 2021. When the medicine feeds the problem; do nitrogen fertilisers and pesticides enhance the nutritional quality of crops for their pests and pathogens? Front. Sustain. Food Syst. *5*. https://doi.org/10.3389/fsufs.2021.701310.

Müller-Motzfeld, G., 2004. Vol. 2 Adephaga 1: Carabidae (Laufkäfer). In: Freude, H., Harde, K.W., Lohse, G.A., Klausnitzer, B., Die Käfer Mitteleuropas, H., Freude, K.W., Harde, G.A. Lohse, Klausnitzer, B. (Eds.), Adephaga 1: Carabidae (Laufkäfer). Spektrum Akademischer Verlag, 2nd ed. Elsevier, Heidelberg. 521 pp.

Östman, Ö., Ekbom, B., Bengtsson, J., 2001. Landscape complexity and farming practice influence biological control. Basic Appl. Ecol. *2*, 365–371. https://doi.org/10.1078/1439-1791-00072.

Parajulee, M.N., Slosser, J.E., 1999. Evaluation of potential relay strip crops for predator enhancement in Texas cotton. Int. J. Pest Manag. *45* (4), 275–286. https://doi.org/10.1080/096708799227680.

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <⟨https://www.R-project.org/⟩>

Rakotomalala, A.A.N.A., Ficiciyan, A.M., Tscharntke, T., 2023. Intercropping enhances beneficial arthropods and controls pests: a systematic review and meta-analysis. Agric. Ecosyst. Environ. *356*, 108617. https://doi.org/10.1016/j.agee.2023.108617.

Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). Ecol. Monogr. *43* (1), 95–124. https://doi.org/10.2307/1942161.

Ropek, D., Jaworska, M., 1994. Effect of an entomopathogenic nematode,Steinernema carpocapsae Weiser (Nematoda, Steinernematidae), on carabid beetles in field trials with annual legumes. Anz. F. üR. Sch. ädlingskunde Pflanzenschutz Umweltschutz *67* (5), 97–100. https://doi.org/10.1007/BF01904698.

Rusch, A., Bommarco, R., Jonsson, M., Smith, H.G., Ekbom, B., 2013. Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. J. Appl. Ecol. *50* (2), 345–354. https://doi.org/10.1111/1365-2664.12055.

Savary, S., Willocquet, L., Pethybridge, S.J., Esker, P., McRoberts, N., Nelson, A., 2019. The global burden of pathogens and pests on major food crops. Article 3. Nat. Ecol. Evol. *3* (3). https://doi.org/10.1038/s41559-018-0793-y.

Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M., Tscharntke, T., 2003. Relative importance of predators and parasitoids for cereal aphid control. Proc. R. Soc. Lond. Ser. B Biol. Sci. *270* (1527), 1905–1909. https://doi.org/10.1098/rspb.2003.2469.

Schmidt, M.H., Roschewitz, I., Thies, C., Tscharntke, T., 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. J. Appl. Ecol. *42* (2), 281–287. https://doi.org/10.1111/j.1365-2664.2005.01014.x.

Smith, B.M., Jones, N.E., 2007. Effects of manipulating crop architecture on weed and arthropod diversity in winter wheat. Aspects of Applied Biology 81, 31.

Sunderland, K., Samu, F., 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. Èntomol. Exp. Et. Appl. *95* (1), 1–13. https://doi.org/10.1046/j.1570-7458.2000.00635.x.

Tamburini, G., Bommarco, R., Wanger, T.C., Kremen, C., van der Heijden, M.G.A., Liebman, M., Hallin, S., 2020. Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci. Adv. *6* (45), eaba1715. https://doi.org/10.1126/sciadv.aba1715.

Tortosa, A., Duflot, R., Rivers-Moore, J., Ladet, S., Esquerré, D., Vialatte, A., 2022. Natural enemies emerging in cereal fields in spring may contribute to biological control. Agric. For. Entomol. *24* (3), 267–278. https://doi.org/10.1111/afe.12490.

Triquet, C., Roume, A., Tolon, V., Wezel, A., Ferrer, A., 2022. Undestroyed winter cover crop strip in maize fields supports ground-dwelling arthropods and predation. Agric. Ecosyst. Environ. *326*, 107783. https://doi.org/10.1016/j.agee.2021.107783.

Wagner, D.L., Grames, E., Foristerb, M., Berenbaumc, M., Stopakd, D., 2021. Insect decline in the Anthropocene: death by a thousand cuts. PNAS *118* (2). https://doi.org/10.1073/pnas.2023989118.

Ward, D.F., New, T.R., Yen, A.L., 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. J. Insect Conserv. 5, 47–53.

Yin, W., Chai, Q., Zhao, C., Yu, A., Fan, Z., Hu, F., Fan, H., Guo, Y., Coulter, J.A., 2020. Water utilization in intercropping: a review. Agric. Water Manag. *241*, 106335. https://doi.org/10.1016/j.agwat.2020.106335.

Yousefi, M., Marja, R., Barmettler, E., Six, J., Dray, A., Ghazoul, J., 2024. The effectiveness of intercropping and agri-environmental schemes on ecosystem service of biological pest control: a meta-analysis. Agron. Sustain. Dev. *44* (2), 15. https://doi.org/10.1007/s13593-024-00947-7.

Zhao, Z.-H., Hui, C., He, D.-H., Ge, F., 2013. Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. BioControl *58* (6), 765–776. https://doi.org/10.1007/s10526-013-9536-9.

Ziesche, T.M., Ordon, F., Schliephake, E., Will, T., 2023. Long-term data in agricultural landscapes indicate that insect decline promotes pests well adapted to environmental changes. J. Pest Sci. https://doi.org/10.1007/s10340-023-01698-2.