META-ANALYSIS



The effectiveness of intercropping and agri-environmental schemes on ecosystem service of biological pest control: a meta-analysis

Maryam Yousefi^{1,2} • Riho Marja³ • Elias Barmettler^{4,5} • Johan Six¹ • Anne Dray¹ • Jaboury Ghazoul¹

Accepted: 17 January 2024 © The Author(s) 2024

Abstract

Plant diversification contributes to the ecological intensification of agroecosystems through pest biocontrol services provision. However, the existing evidence for the effectiveness of plant diversification in enhancing pest biocontrol services is highly uncertain across features of plant diversity and biodiversity characteristics. We undertook a comparative meta-analysis focusing on three essential crops (wheat, maize, and soybean) to investigate how diversification schemes in-field (intercropping) and Agri-environmental scheme (AES) around the field (flower strip, hedgerow and field margin) affect arthropod abundance. A random effects analysis was used to determine the role of 10 key factors underlying the effectiveness of plant diversification including biodiversity level and habitat, main and companion plant species, intercropping arrangement, the growth stage of the main crops, type of AES planting scheme, AES planting width, distance from AES plantings and geographical latitude. The overall results revealed that intercropping reduced herbivore and boosted predators and parasitoids abundance significantly, while AES successfully increased predators but not herbivores. Maize intercropping with legume and non-legume plants and row intercropping allowed for effective pest management. The abundance of predators increased in wheat fields immediately adjacent to planting around the field (AES), but this effect declined beyond 5 m from the flower strips. Our results suggest that the response of arthropod abundance to plant diversification is a compromise between spatial management scale, ecological characteristics of arthropod and plant diversification features. These results offer promising pathways for optimizing plant diversification schemes that include functional farm biodiversity across spatial and temporal scales and designing multi-functional landscapes.

 $\textbf{Keywords} \ \ A groecology \cdot A gricultural \ sustainability \cdot Cereal \cdot Diversified \ farming \ systems \cdot Farmland \ biodiversity \cdot Multifunctional \ landscapes \cdot Quantitative \ synthesis$

Maryam Yousefi Maryam. Yousefi@zalf.de

> Riho Marja riho.marja@ecolres.hu

Elias Barmettler elias.barmettler@agroscope.admin.ch

Johan Six johan.six@usys.ethz.ch

Anne Dray anne.dray@usys.ethz.ch

Jaboury Ghazoul @env.ethz.ch

Published online: 26 February 2024

- Ecosystem Management, Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zurich, Universitätsstr. 16, 8092 Zürich, Switzerland
- ² Leibniz Centre for Agricultural Landscape Research, Eberswalder 84, 15374 Müncheberg, Germany
- 3 "Lendület" Landscape and Conservation Ecology, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány u. 2-4, 2163 Vácrátót, Hungary
- Plant-Soil Interactions Group, Agroscope, Switzerland
- Department of Plant and Microbial Biology, University of Zurich, Rämistrasse 71, 8006 Zürich, Switzerland



15 Page 2 of 15 M. Yousefi et al.

1 Introduction

Agroecosystems in the context of current discussion on socio-ecological transitions are increasingly expected to integrate biodiversity conservation alongside demands to meet current and future food needs (Chappell and LaValle 2011; Fischer-Kowalski et al. 2012; Darvishi et al. 2020; Yousefi et al. 2020). The existing evidence implies that the strategies to address both conservation and food production are not necessarily mutually exclusive and can be reconciled using the adaptation of appropriate agricultural habitat measures (Chappell and LaValle 2011; Yousefi et al 2021; Darvishi et al 2022). Diversified farming systems (DFS) are increasingly argued to be a credible alternative to conventional intensified agriculture by facilitating a more sustainable and secure global food system (Feliciano 2019; Jones et al. 2021; Rosa-Schleich et al. 2019). Agrobiodiversity is promoted by DFS at multiple spatial scales, including within fields (e.g. composting, intercropping, agroforestry), across entire fields (e.g. crop rotations, cover cropping, fallowing) and along field margins (e.g. hedgerows, border plantings, grass strips) (Kremen et al. 2012). Plant diversification as one of the DFS' strategies has been shown to restore vital ecosystem services such as pest regulation by supporting arthropod community trophic structures (Albrecht et al. 2020; Puliga et al. 2022; Arnott et al. 2022), which are at risk of deteriorating or becoming less effective in response to future climate changes (Lin 2011). Arthropod communities play a crucial role in agroecosystems, particularly in the context of biological pest control, which involves the interaction

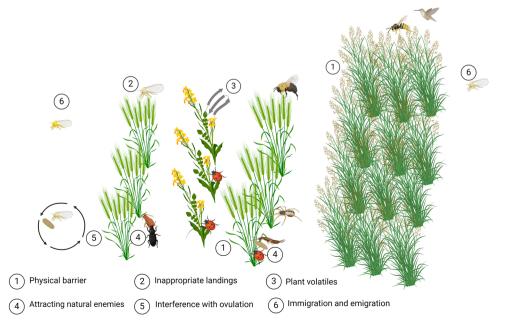
between agricultural pests, such as herbivores, and their natural enemies (Gurr et al. 2019; Lu et al. 2022). Plant species diversity in agroecosystems can minimize the impact of pests by several mechanisms, including physical barriers, inappropriate landing, emissions of volatile organic compounds (VOCs), supporting natural enemies and interference with ovulation and migration (Figure 1).

Physical barriers mechanism Theoretically, companion plants might function as physical barriers and conceal the host crop from herbivores. This barrier effect limits colonization and explains the pattern of decreased arthropod activity (CÁrcamo and Spence 1994). It makes the host plants harder to find and alters their recognition (Poveda and Kessler 2012).

Inappropriate landing Some herbivores may have difficulty locating their host plants that are intercropped or mixed with others when companion nonhost plants are cultivated with the main crop. Plant diversification effects host plant findings by giving arthropods a choice of appropriate and inappropriate plants (Parsons et al. 2007). They have to spend additional energy and time looking for it on the wrong host plant, which is more challenging to locate. In this context, Finch and Collier (2000) described this host plant selection mechanism as the appropriate/inappropriate landings theory.

Volatile organic compounds (VOCs) emission Plant diversification affects host plant selection by disrupting host habitat location and host acceptance process, mainly attributed to releasing repellent VOCs by companion plants (Ben-Issa et al. 2017; Bianchi and Wäckers 2008; Zhou et al. 2013a).

Fig. 1 The schematic illustration shows an intercropping field with AES and the mechanisms of the effect of plant diversification on farm arthropods (source: authors, created with BioRender.com).





Volatiles are the metabolites that plants emit into the atmosphere and have given plants ways to overcome the difficulties of being immobile and grounded in the soil (Baldwin 2010). Hence, the behaviour of arthropods and their natural enemies is frequently influenced by nonhost plants' volatiles (Zhou et al. 2013a).

Resources for natural enemies Root (1973) detected fewer pests in weedy plantings and hypothesized plant diversification may support natural enemies and provide shelter and resources to reproduce and reinforce herbivore control (Bianchi and Wäckers 2008; Blubaugh et al. 2021; Schütz et al. 2022; Yang et al. 2022). These suggested mechanisms have played a significant role in managing agroecosystems to advance biological control and conservation (Ben-Issa et al. 2017).

Interference with ovulation Arthropods need specific conditions for ovulation and oviposition, and nearby nonhost plants may change their ovulation behaviour. They also may alter their distribution, position or quantity of eggs laid on a plant when other nonhost plant species are present (Hooks and Johnson 2003). Microclimate parameter changes may also disturb herbivores' feeding and reproductive behaviour (Baldwin 2010).

Immigration and emigration Some herbivores are less likely to remain near their host habitat when surrounded by nonhost plants. They may relocate to another environment with more resources and host plants after interacting with plenty of nonhost plants (Hooks and Johnson 2003; Mansion-Vaquié et al. 2020; Lopes et al. 2015).

However, the microhabitat parameters such as soil moisture, solar radiation temperature, wind speed and light penetration may change due to intercropping, making the habitat less appropriate for particular species (Knörzer et al. 2011; Lopes et al. 2016). Since insects are ectotherms, even little changes in the air temperature can significantly impact their metabolic, activity, and feeding rates (Liu et al. 2018).

Previous studies have reported positive effects of plant diversification on farm biodiversity (Beillouin et al. 2019; Beillouin et al. 2021; Rosa-Schleich et al. 2019). However, some studies have also found that the effects of plant diversification may depend on ecological characteristics of arthropod, trophic level (Letourneau et al. 2011), host specialization (Chaplin-Kramer et al. 2011; Dassou and Tixier 2016), specialization (which shows whether the arthropod is a specialist or a generalist) (Dassou and Tixier 2016) and arthropod habitat (vegetation, ground, or soil-dwelling) (Liu et al. 2018; Marja et al. 2022). For instance, Dassou and Tixier (2016) emphasized that specialist and generalist arthropod differed in their response to plant diversification. They

showed that only the abundance of generalist predators had a significant positive response to plant diversification. Marja et al (2022) found that the abundance of vegetation-dwelling but not ground-dwelling arthropods increased under agricultural landscape diversification.

The role of moderator factors such as crop species and the design of plant diversification schemes could be overlooked in an evaluation of the biodiversity response only based on arthropod characteristics (Albrecht et al. 2020, Brooker et al. 2015; Lopes et al. 2016; Zhou et al. 2013b). For instance, Albrecht et al. (2020) showed that the effectiveness of plant diversification might decline with increasing distance from an agroecological intervention. Moreover, uncertainty exists over the effectiveness of plant diversification in crop diversification strategies (Kebede et al. 2018) and spatial scales (e.g. in- and around-crop fields) (Letourneau et al. 2011). Limited understanding of the relative significance of the diversification scheme and its contribution to farm biodiversity resilience and pest control potential makes the development of reliable strategies challenging and is a critical obstacle to farmer adoption (Albrecht et al. 2020; Kleijn et al. 2019). This highlights the need to investigate the role of plant diversification effectiveness drivers in enhancing pest regulation based on arthropod and diversification features.

In the current study, we aimed to rigorously explore the effects of in-field and around-field plant diversification schemes on arthropod abundance in wheat, maize, and soybean crops. To achieve this goal, we conducted a comprehensive comparative meta-analysis, based on two sets of databases. The first set encompassed global studies comparing monocropping and intercropping as in-crop field schemes, while the second set included studies from around the world comparing monocropping with flower strips, hedgerows, and field margins as plant diversification around-crop field schemes (hereafter agri-environmental scheme (AES)).

Moreover, we evaluated key factors underlying the effectiveness of plant diversification on arthropod abundance. These factors include ecological characteristics of arthropods (biodiversity level and habitat), features of plant diversification (main and companion plant species, intercropping arrangement, the growth stage of the main crops, type of AES planting scheme, AES planting width, distance from AES plantings) and geographical latitude.

The features of plant diversification and ecological characteristics of arthropods were strategically selected due to their associations with established mechanisms such as physical barriers, inappropriate landing, VOC emissions and resource provisioning for natural enemies. By anchoring our study in these mechanisms, we sought to reveal the intricate relationships between plant diversification, arthropod traits and underlying ecological processes. The inclusion of geographical latitude adds an additional layer of complexity,



allowing us to explore how regional variations may influence the outcomes of plant diversification strategies on arthropod abundance.

The findings of this study help to predict the most reliable plant combination, intercropping design and type of AES planting in order to achieve the desired outcome.

2 Methods

2.1 Data collection

We systematically searched in April 2022, following the guidelines of PRISMA guidelines (preferred reporting items for meta-analyses). We used Web of Science Core Collection, Scopus and Google Scholar search engines to find studies based on the search syntax outlined in Table 1. The search yielded 1557 publications (Web of Science (580), Scopus (677), Google Scholar (300)). We focused on the first 300 relevant Google Scholar results to reduce the proportion of grey literature in the search results (Haddaway et al. 2015; Sinthumule 2023). The titles and abstracts of all studies were independently checked for relevance by two qualified reviewers during the primary screening and a total of 227 publications were retained based on the title and the abstract screening. The full texts of these articles were read in detail and a total of 43 (21 studies on intercropping and 22 on AES) articles were included in the synthesis. Paper screening and selection procedure are presented in PRISMA diagram (Fig. S1) (see the maps showing the distribution of location in Fig. S2). Our inclusion and exclusion criteria were as follows: The studies comparing monoculture (as the control system) and intercropping (as the treatment system) were considered. We also selected studies comparing fields adjacent to AES treatment to fields without AES as the control system. Wheat, maize and soybean had to be included in the crop system. Only data from the primary agricultural field experimental studies were included. We excluded studies published in languages other than English, as well as those lacking new experimental data such as reviews or book chapters. We excluded primary studies conducted in laboratories or greenhouses, single observations or missing an appropriate control. The articles described the plant diversification experiment and reported a quantitative comparison of plant diversification outcomes compared to a relatively simplified farming system or natural habitat. The studies that did not provide enough information to differentiate the intervention were excluded. Other farm practices such as applying fertilizer, pesticides, crop irrigation, crop rotation, crop residue management and soil tillage regime had to be similar between plots, ensuring that the treatments were affected only by intervention. We limited our search to studies published after 1999 because most countries started reforming their agricultural policies in the 1990s (McGurk et al. 2020), and the lack of prior research before this date hinders the credibility and scope of our study. The studies that examined intercropping between different cultivars were excluded. We excluded the studies that failed to report mean values, the number of replicates and at least statistical parameters (standard deviation or error, confidence intervals).

The following additional criteria were also considered: if the study was conducted in multiple geographical areas, multiple companion crops, multiple AES types and multiple arthropod sampling dates in different growth stages of the main crops, we extracted each as a separate record. If the article did not specify the sampling date or, in the case of replicating the sampling procedure, we considered the mean of the first and last sampling date. If the study examined transgenic and non-transgenic crop species, we extracted data from non-transgenic species. If the study reported the results in multiple years, we extracted last year's data.

We extracted data from text, tables or graphs using Web-PlotDigitizer (Rohatgi 2015). Table 2 shows a summary of variables that have been extracted from the studies. We generated two additional moderators based on the arthropods' functional levels. The moderators included the level of biodiversity (community and species level) and arthropods' habitat (vegetation and ground-dwelling) since plant diversification schemes influence functional groups differently (Marja et al. 2022).

Table 1 The literature search syntax.

Plant diversification scheme	Search syntax
Intercropping (in-field)	"intercrop*" OR "crop diversification*" OR "polyculture" OR "crop mixture" OR "mixed crop*" OR "crop divers*" OR "crop* strip"
AES (around-field)	"agri-environment*" OR "flower strip" OR "riparian buffer" OR "riparian zone" OR "set aside" OR "hedgerow" OR "field margin" OR "buffer strip."
Biodiversity	"arthropod*" OR "insect*" OR "beetle*" OR "carabid*" OR "spider*" OR "hoverfl*" OR "syrphid*" OR "parasitoid*" OR "wasp" OR "pollinat*" OR "bee" OR "bumble*" OR "syrph*" OR "butterfl*" OR "predat*" OR "biological control*" OR "pest control*" OR "natural en*" OR "pest manag*"
Main crops	"Wheat" OR "maize" OR "soybean" OR "corn"



Table 2 Summary of moderator variables.

Moderator	Intercrop	AES	Definition	Data type/unit
Geographical latitude	✓	✓	Geographical latitude of the experimental site	Numerical (decimal degrees)
Main crop species	✓	✓	Maize, soybean or wheat	Categorical
Companion crop	✓	✓	Whether companion crop species are legume or non-legume	Categorical
Spatial intercropping arrangement	✓		In which way the two species were intercropped: - Strip intercropping: two species cultivated in alternative strips and at least one strip includes more than one row; -Row intercropping: two species cultivated in alternate rows; -Fully mixed intercropping: two species cultivated in the same field without any distinct row or strip pattern.	Categorical
Growth stage of the main crops	✓		Sampling date after planting the main crop (week)	Numerical (week)
Functional level	✓	✓	Herbivore, predators, pollinator, parasitoide, detritivores	Categorical
Type of plant around the field		\checkmark	flower strip, hedgerows and field margin	Categorical
AES width		✓	1–5, 5–10, >10	Categorical

2.2 Effect size

The log response ratio as a measure of effect size was used to estimate the outcome of an experiment as the log-proportional change between the means of treatment and the control group. The log response ratio has a variety of advantageous properties as an effect size measure. First, the log response ratio is related directly to the percentage change between the measure and the control experiment (Hedges et al. 1999). Moreover, the log response ratio is comparatively unaffected by the method used to assess the outcome variable. For instance, some studies used a 2-week study period, while others used a several-month study period or reported the abundance of biodiversity in different units (e.g. m², per crop, per ten crops).

The following formulas were used for calculating the log response ratios (R_b) (Hedges et al. 1999):

$$ln(R_b) = ln(\frac{\overline{X}_T}{\overline{X}_C})$$

where \overline{X}_T is mean of treatment and \overline{X}_C is mean of the control group.

2.3 Correction for effect size

The log response ratio is biased when quantifying the outcome of studies with small sample sizes (in this study replication number). This can yield erroneous variance estimates when the scale of study parameters is near zero. Therefore, we used variance correction based on Lajeunesse (2015).

Correction for effect size

$$lnR^{\Delta} = ln(R_b) + 0.5 \left[\frac{(SD_T)^2}{N_T \overline{X}_T^2} + \frac{(SD_C)^2}{N_C \overline{X}_C^2} \right]$$

The variance is

$$SD_{pooled} = \sqrt{\frac{\left(N_{T} - 1\right)SD_{T}^{2} + \left(N_{C} - 1\right)SD_{C}^{2}}{N_{T} + N_{C} - 2}}$$

$$Variance \ ln \left(R_b\right) = \frac{SD_{pooled}^2}{N_T \overline{X}_T^2} + \frac{SD_{pooled}^2}{N_C \overline{X}_C^2}$$

Corrections for the variance for small sample size (based on Lajeunesse 2015)

$$Variance \ lnR^{\Delta} = Variance \ ln\left(R_b\right) + 0.5 \left[\frac{\left(SD_T\right)^4}{N_T^2 \, \overline{X}_T^4} + \frac{\left(SD_C\right)^4}{N_C^2 \, \overline{X}_C^4}\right]$$

2.4 Publication bias

In this section, the statistical methods developed to provide rigorous assessments for publication bias. The functions regtest and trimfill which serves the dual purpose of detecting and adjusting for publication bias commonly recommended to use this method as part of a sensitivity analysis (Lin et al. 2018), are not currently supported within the R (R Development Core Team 2022) package metafor (Viechbauer 2010) when using the rma.mv function (Anton et al. 2019). Therefore, possibility of publication bias was assessed based on Egger's regression test (Egger et al. 1997; Sterne and Egger 2005) by modifying the models to



incorporate the standard error of the log RR as a moderator. Egger's regression test is one of the most commonly used methods to examine funnel plot asymmetry (Pustejovsky and Rodgers 2019).

The possibility of publishing bias was identified for each functional group separately (herbivores, predators and parasitoids) if the intercept of the regression test considerably differed from zero at $P \le 0.05$. If possible, bias was identified, using the rstandard function in R, we investigated the effect sizes with standardized residual values greater than three to check for possible influential outliers (Habeck and Schultz 2015). The potential influential outliers were eliminated to adjust for publication bias. We then again re-ran the mixed-effects model to evaluate the sensitivity of the model by comparing fitted random effects models with and without the potential outliers. However, the outcomes of the models did not change when we tested. Finally, our sensitivity analyses revealed that the results are robust to publication bias.

2.5 Meta-analysis

Standard meta-analysis models assume that the observed effect sizes or results from a collection of studies are independent of one another. In reality, this presumption is frequently violated. In the current study, multiple treatment groups (main crops, location and sampling distance towards the field centre) are compared to a common control group or extracted from the same publication. Such data are applied repeatedly to calculate the observed effect sizes. In this circumstance, sampling errors may be correlated in multiple treatment experiments (Viechtbauer and Viechtbauer 2015). To overcome this issue, multivariate/multilevel models were developed based on rma.mv function, which uses a Waldtype test to establish statistical significance. The metafor package (Viechbauer 2010) in R was used to conduct two separate meta-analyses in and around the field.

To account for heterogeneity both between and within studies (in case multiple observations were extracted from the same publication), we specified the effect size and the study identification (ID) as random effects in our model (Tamburini et al. 2020). The model that included a nested random structure random=list(~1| Study ID,~1| Effect size ID) yielded the lowest Akaike information criterion (AIC) score (Burnham and Anderson 2002) compared with the other candidate structures, and was therefore retained (table S1).

Twenty-one published articles comprising 198 observations were recorded, consisting of field experiments on intercropping as treatment and sole cropping as control. The functional groups of this dataset included detritivores, herbivores, predators and parasitoids. We excluded detritivores and parasitoids from further analysis due to the limited number of observations. In intercropping, soybean has

been utilized as a companion crop, not as the primary crop. Hence, we could not identify any record for soybean as the main crop. Different types of intercropping were implemented, depending on the species used. Row intercropping was the most common type, followed by strip cropping.

Another meta-analysis was conducted based on 22 papers and 122 observations, comparing AES schemes vs monocropping. Herbivores, predators, and parasitoids were identified as functional groups, Due to the limited number of observations, we had to limit our further analysis to predators. Enhanced plant diversification under AES was reported mainly through flower strips (more than half of the studies), followed by grass margins and hedgerows.

To understand the key factors that may influence the response of farmland arthropods, we performed subgroup analysis for categorical variables as fixed factors in the mixed-effects model to investigate possible variation in the pooled effect size. This analysis included the following variables: main crop species, companion crop, intercropping arrangement, AES planting width (can influence the extent to which they provide habitat and resources for arthropods), and type of AES planting, where at least three studies reported data to ensure adequate sample size. As only one study considered mixed intercropping and only one reported the abundance of predators at the species level, we did not include these variables in our intercropping subgroup analysis. Furthermore, we did not perform a subgroup analysis within the parasitoid functional group due to the limited number of observations.

Additionally, we ran meta-regression models to investigate the possible correlation between arthropod abundance and the growth stage of the main crops in intercropping experiments and between arthropod abundance and sampling distance from AES plantings.

According to the latitudinal biotic interaction hypothesis (LBIH), which revealed the intensity of biotic interactions is maximum in tropical areas and decreases from low to high latitudes (Zvereva et al. 2020; Zvereva and Kozlov 2021), we also investigated how arthropod abundance change across latitude under intercropping (in each hemisphere separately). We did not examine the effect of latitude on AES effectiveness because the majority of the observations in AES management were conducted in Europe.

3 Results

3.1 Overall effects of diversification schemes on herbivores, predators and parasitoids

Overall summary effect size in intercropping across all arthropod functional groups (detritivores, herbivores, predators and parasitoids) revealed a negative but non-significant



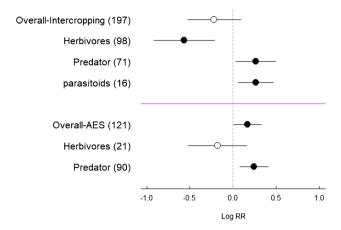


Fig. 2 Mean effect size (log scale response ratio) and $\pm 95\%$ confidence intervals of arthropod abundance depends on the functional group classified by herbivores, predators, and parasitoids across intercropping and AES. The dashed line indicates zero effect size. The number in the parentheses indicates the number of observations for each comparison. The observations of detritivores in intercropping and parasitoids in AES were removed due to limited sample size.

effect (Figure 2). Further investigation based on functional groups demonstrated that herbivore abundance was significantly lower under intercropping, which greatly affected the negative pooled effect size. The abundance of predators and parasitoids increased under intercropping.

Overall, AES significantly boosted the abundance of arthropods. Most observations were found for predators, which significantly increased under plant diversification schemes. However, the abundance of herbivores varied widely and was not significantly different between diversified and simplified farming systems.

3.2 The role of plant diversification and ecological characteristics of arthropod under intercropping

Intercropping in maize fields strongly suppressed herbivores and increased predator abundance (Figure 3 and Table S2), suggesting that diversification schemes achieved the desired outcome in maize intercropping. However, the effect of intercropping in wheat fields was variable and statistically non-significant for both herbivores and predators. Both non-legume and legume intercrops showed a significant positive impact on herbivore suppression. Non-legume intercrops significantly supported predators. In contrast, legume crops appeared to have a variable influence on predatory arthropods. Moreover, row intercropping reduced herbivores' outbreaks and enhanced predator abundance. There was no agreement between studies, which reported the effect of strip intercropping on herbivores and predator abundance.

The results from our meta-analysis demonstrated that ground-dwelling predators and herbivores' abundance were more likely to change under intercropping. However, vegetation-dwelling arthropods showed no significant change under intercropping measures. Intercropping significantly decreased herbivores on community species and levels (Table 2S).

3.3 The role of plant diversification and ecological characteristics of arthropod under AES

Plant diversification under AES in wheat fields positively affected predators, but evidence from maize and soybean

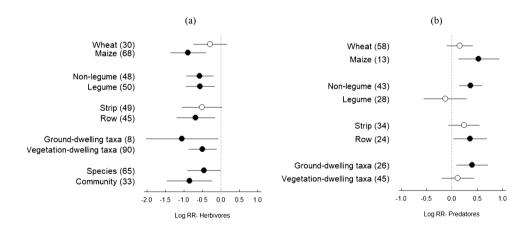


Fig. 3 Intercropping mean effect size (log scale response ratio) and $\pm 95\%$ confidence intervals of arthropod abundance depends on moderators across herbivores (a) and predators (b). The dashed line indicates zero effect size. The number in the parentheses reflects the number of observations for each comparison.



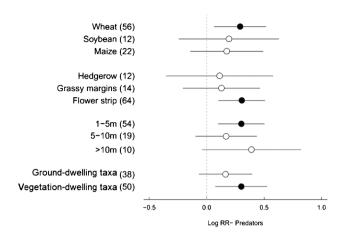
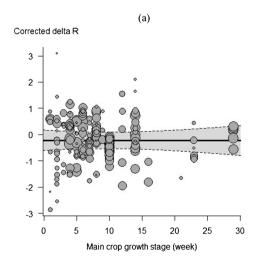
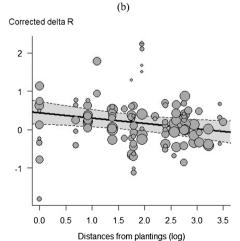


Fig. 4 AES mean effect size (log scale response ratio) and $\pm 95\%$ confidence intervals of arthropod abundance caused by different types of the main crop, type of AES, and width of AES and habitat of arthropods. The dashed line indicates zero effect size. The number in the parentheses reflects the number of observations for each comparison.

field experiments failed to show statistically significant effects (Figure 4 and Table S3). Predator abundance was significantly higher in fields with flower strips, while the mean effect sizes of hedgerows and grassy margins were highly variable between studies. The abundance of predators increased in a 5-m-planting width; however, this effect declined beyond 5 m from the AES plantings. Both vegetation and ground-dwelling predator taxa showed positive mean effect sizes, though the effect was significant only for vegetation-dwelling taxa.

Fig. 5 a The main crop growth stage (week). b Distance from AES plantings for the overall data set. Linear meta-regressions are shown as solid black lines and grey area represents 95% Cis.





3.4 The role of the growth stage of the main crops, sampling distance from AES plantings and geographical area

The correlation between the main crop growth stage and arthropod abundance under intercropping did not show a consistent result across studies (P = 0.9813), while arthropod abundance tended to decrease with the sampling distance from AES plantings (0.0192) (Figure 5 and Table S4).

We explored the effect of plant diversification across latitudinal gradients as the sources of variation in response ratio. There was no indication that the effect of plant diversification varied across latitudinal gradients in the Northern (P = 0.4392) and Southern (P = 0.746) hemispheres (Table S4).

4 Discussion

4.1 The effect of plant diversification on arthropod abundance in- and around-crop fields

Our quantitative synthesis demonstrates a generally positive effect of plant diversification on herbivore suppression and predator enhancement under intercropping. AES management increased predator abundance, but the effect on herbivore suppression was highly variable. This result aligns with Letourneau et al (2011), who showed that flowering plants in or around the crop field significantly increase natural enemies. In our meta-analysis, stronger negative effects on herbivores under intercropping than AES were detected, which is consistent with Dassou and Tixier (2016). Moreover, the positive effects of diversification schemes on predators were stronger in intercropping than AES. This highlights the general effect of scale and type of diversification on the response by arthropods.



4.2 The role of moderator factors in intercropping

Intercropping in wheat fields failed to reduce pests or increase predators. Bulson et al. (1997) argued that wheat intercropping provided other benefits such as increased land utilization efficiency or weed suppression. Possible explanations for this result include the date of cultivation and resource concentration theory. The cultivation date determines whether companion plants grow and bloom at a time relevant for pest suppression or control (Altieri et al. 1978); if there are flowers to serve as a source of nectar for insects and other arthropods (Hatt et al. 2019).

Resource concentration theory (Root 1973, Skelton and Barrett 2005) explains that monophagous or specialized herbivores are more likely to survive and reproduce near host crops and monocultures.

In this study, the majority of studies reported arthropod abundance at the community level, which may choose companion crops as hosts and wheat as nonhost plants. Therefore, there may not be a difference in herbivore abundance between intercropping and monoculture wheat-based systems, or it may even be greater in intercropping systems based on wheat.

Plant diversification based on both legume and non-legume companion plants increased herbivore suppression. However, predator abundance was not significantly different between crops with non-legume companion crops. The species of non-legume plants and the lack of temporal overlap between the main crops and companion crops may dissipate the natural enemies (Hatt et al. 2019; Parajulee and Slosser 1999) and may also explain part of the high variability observed across studies.

While we did not detect consistent effects in strip design, the positive effect of the row intercropping pattern on pest control services provision was found in support of the resource concentration hypothesis (Root 1973). When food sources are not concentrated, as they are in monoculture, it is difficult for a herbivore to discover its target host plant when two plant species are grown in alternate rows. On the other hand, based on supporting natural enemies mechanism, plant diversification provides the amount of food and shelter available to predators, as well as enhancing their host range and host-finding abilities (Smith and McSorley 2000).

This can justify the effectiveness of row intercropping because arthropods showed a significant positive change compared to strip intercropping. This emphasizes the necessity to discover the drivers that cause intercropping to succeed or fail in promoting pest control services.

Both ground and vegetation-dwelling herbivores were affected by intercrops. However, there was wide variability in the response of ground-dwelling herbivores. We did not detect a consistent effect on vegetation-dwelling predators while ground-dwelling predators increased under plant

diversification. The largest change in ground-dwelling species was with intercropping. One of the possible reasons is that plant diversification reduces arthropods' movement rates and decreases their colonization due to the physical barrier mechanism (CÁrcamo and Spence 1994).

The most effective mechanism in vegetation-dwelling herbivores decline can be inappropriate landing in which herbivores have trouble host-plant findings by giving arthropods a choice of companion crops (Parsons et al. 2007). However, the response of herbivores to plant diversification was different at the community and species levels. The response was negative and significant at both levels, but it was stronger at the community level. We could not determine the influence of plant diversification based on generalist herbivores or predators because most articles reported arthropod abundance on the community level.

There was no conclusive evidence that plant diversification impacts herbivores and predator variation over the main crop growth stages. One possible explanation for this finding is that we investigated it for the entire dataset, which may differ between main crop species or functional groups. However, because of the lack of sufficient observations for some moderators, we could not proceed further.

A non-significant but marginal increase in arthropods was seen as latitude increased in the intercropping studies. However, it must be addressed in future studies before hard conclusions can be made.

4.3 The role of moderator factors in AES

Although we found a positive effect of plant diversification on predator abundance under AES, the effect in maize and soybean fields adjacent to AES was highly variable. This is a crucial finding as it offers empirical evidence that AES scheme can increase natural enemies of pests adjacent to specific crops. Koji et al (2007) showed that while AES supported a higher abundance of predators, they are not necessarily inclined to move to the adjacent maize fields. The observed variability might also be attributed to different predator behaviours at different maize growth stages. For instance, Varchola and Dunn (2001) found that carabid emergence rates varied with corn maturity. Our meta-analysis demonstrated a positive effect of flower strips on predator enhancement compared to hedgerows and grassy margins. Flower strips are often selected based on the requirements of the target natural enemy, while this is usually not a consideration when implementing hedgerows or grassy field margins (Albrecht et al. 2020; Tschumi et al. 2016). Moreover, AES planting width of up to 5 m leads to a consistent increase in the abundance of predators in crops, but larger widths did not have a consistently positive effect on enhanced



predators in crops. This might be because predators might preferentially remain in the larger AES plots instead of moving into the crop field. The wide confidence interval for AES interventions with widths larger than 10 m might also be due to the relatively small number of observations, and hence this conclusion should be treated with caution. The result of the model for sampling distance from planting schemes showed that the abundance of arthropods declined as the sampling distance increased. A similar pattern was observed by Albrecht et al (2020), who stated that pollination declined with increasing distance to AES. Batáry et al. (2012) emphasized that AES at the edges offer additional food supply and niches for different species to live in, attributable to the diversity and abundance of plants. Hence, this is where the highest abundance of arthropods would be expected.

4.4 The role of moderator factors in intercropping and AES

Understanding the complex mechanisms influencing arthropod dynamics in both intercropping and AES, involves an exploration of spatial arrangements, temporal variations and the distinct characteristics of interventions. Regarding the spatial arrangement factor, the higher efficiency of row intercropping over strip intercropping is paralleled by the significant influence of distance to AES. This calls for an exploration of how similar spatial dynamics in across diverse agricultural practices, and affect arthropod behaviour. Examining temporal considerations reveals that the cultivation date in intercropping plays a pivotal role, determining the presence of flowers for arthropod sustenance. AES interventions, on the other hand, show different results in different stages of maize growth, highlighting the significance of comprehending predator behaviours across growth stages. Furthermore, the positive effect of flower strips on predator abundance contrasts with the varied impact of non-legume companion crops in intercropping. Here, we explore how the selection of interventions based on the requirements of natural enemies influences outcomes. The efficiency of row intercropping echoes the positive effect observed with shorter distances to AES. Both scenarios concentrate resources, facilitating herbivore suppression and predator enhancement. This points to the significance of resource concentration in determining the success of pest control strategies. While predators benefit from AES, their response differs in intercropping with wheat. Potential factors contributing to this distinction include resource availability, habitat suitability or the scale of interventions. Investigating these differences sheds light on the nuanced interactions between predators and interventions.

Our exploration of arthropod dynamics reveals interconnected themes across intercropping and AES. By considering

spatial, temporal and intervention-specific factors, we gain a holistic understanding of the intricate relationships between herbivores, predators and agricultural practices.

4.5 Limitations of the study

In the selected studies, we identified two predominant experimental scenarios: either no fertilizers, pesticides or insecticides were applied, creating a controlled environment for studying the effects of plant diversification; or, in contrast, all fields were conventionally treated with pesticides. Therefore, our analysis was constrained by the available data and the role of pesticides or insecticides as confounding factor was not considered.

In our study, we aimed to maintain a focused and streamlined analysis by employing one moderator in each metaanalysis. While we recognize that interactions among various factors can add complexity to the interpretation, our decision to use a single moderator enhanced clarity and reduced the risk of overfitting the model.

While we acknowledge AES age and plant species on the outcomes of the plant diversification schemes, there can be a time lag between AES implementation and observable ecological benefits. However, in the context of our study, the inclusion of these factors was not possible due to limitations in available data.

5 Conclusion

Our meta-analysis revealed how arthropod functional groups changed under agricultural diversification across a broad range of cropping systems and types of plant diversification. Our results lend some support to the theoretical prediction in terms of pest regulation services such as the resource concentration hypothesis (Root 1973) and inappropriate landing (Finch and Collier 2000). Here, we show for the first time that the effect of plant diversification on biological control services is a compromise between the spatial scale of interventions, ecological characteristics of arthropod and plant diversification features. This emphasizes the need to investigate these factors when designing agricultural schemes to support pest regulation services. The quantified ecological effects of intercropping and AES on pest regulation services provided in this study open up several promising pathways toward optimizing agricultural measures: stakeholders must consider the appropriate spatial scale to foster suitable farm biodiversity strategies; different combinations of plant species diversity and design have very variable outcomes for arthropod abundance and pest control, and this needs to be considered in the context of the impact on crop production. Our findings highlight the potential benefits of implementing



in-field and around-field plant diversification strategies in assisting policy makers in enhancing biodiversity alongside demands to meet current and future food demands.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/s13593-024-00947-7.

Acknowledgements This research project was part of the Biodiversity & Resilience in Crop Production project (1-007514) funded by Bayer AG. However, we would like to clarify that the funding organization played no role in the design of the study, data collection, analysis, interpretation of results, or the writing of this manuscript.

Authors' contributions MY conceptualized and designed the study, performed the literature review, data extraction, meta-analysis, and prepared the first draft of the manuscript. RM designed the study, performed the meta-analysis, and interpreted the results. EB contributed to study screening and data extraction. JS and AD contributed to the revision. JG interpreted the results and contributed substantially to the revision.

Funding Open access funding provided by Swiss Federal Institute of Technology Zurich This study was part of the Biodiversity & Resilience in Crop Production project (1-007514) funded by Bayer AG. RM has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 101027920.

Data availability All data generated or analysed during this study are uploaded in Figshare https://figshare.com/s/f917292ba99fa1aec4ea

Declarations

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication By submitting this manuscript for publication, we, the authors, provide our consent for its publication in the designated journal. We affirm that this manuscript is original, has not been previously published, and is not under consideration for publication elsewhere. We take responsibility for the content and integrity of the manuscript and declare that all the listed authors have made substantial contributions to the study.

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Albrecht M, Kleijn D, Williams NM et al (2020) The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis. Ecol Lett 23(10):1488–1498. https://doi.org/10.1111/ele.13576
- Altieri MA, Francis CA, Van Schoonhoven A et al (1978) A review of insect prevalence in maize (*Zea mays* L.) and bean (*Phaseolus vulgaris* L.) polycultural systems. Field Crops Res 1:33–49. https://doi.org/10.1016/0378-4290(78)90005-9
- Anton A, Geraldi NR, Lovelock CE et al (2019) Global ecological impacts of marine exotic species. Nat Ecol Evol 3:787–800. https://doi.org/10.1038/s41559-019-0851-0
- Arnott A, Riddell G, Emmerson M, Reid N (2022) Agri-environment schemes are associated with greater terrestrial invertebrate abundance and richness in upland grasslands. Agron Sustain Dev 42(1):6. https://doi.org/10.1016/j.landusepol.2009.07.009
- Baldwin IT (2010) Plant volatiles. Curr Biol 20(9):R392–R397. https://doi.org/10.1038/s41559-019-0851-0
- Batáry P, Holzschuh A, Orci KM (2012) Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. Agric Ecosyst Environ 146(1):130–136. https://doi.org/10.1016/j.agee.2011.10.018
- Beillouin D, Ben-Ari T, Makowski D (2019) Evidence map of crop diversification strategies at the global scale. Environ Res Lett 14(12):123001. https://doi.org/10.1088/1748-9326/ab4449
- Beillouin D, Ben-Ari T, Malézieux E et al (2021) Positive but variable effects of crop diversification on biodiversity and ecosystem services. Global Change Biol 27(19):4697–4710. https://doi.org/10.1111/gcb.15747
- Ben-Issa R, Gomez L, Gautier H (2017) Companion plants for aphid pest management. Insects 8(4):112. https://doi.org/10.3390/insec ts8040112
- Bianchi FJ, Wäckers FL (2008) Effects of flower attractiveness and nectar availability in field margins on biological control by parasitoids. Biol Control 46(3):400–408. https://doi.org/10.1016/j.biocontrol.2008.04.010
- Blubaugh CK, Asplund JS, Smith OM, Snyder WE (2021) Does the "Enemies Hypothesis" operate by enhancing natural enemy evenness? Biol Control 152:104464. https://doi.org/10.1016/j.biocontrol.2020.104464
- Brooker RW, Bennett AE, Cong WF et al (2015) Improving intercropping: a synthesis of research in agronomy, plant physiology and ecology. New Phytol 206(1):107–117. https://doi.org/10. 1111/nph.13132
- Bulson HAJ, Snaydon RW, Stopes CE (1997) Effects of plant density on intercropped wheat and field beans in an organic farming system. J Agric Sci 128(1):59–71. https://doi.org/10.1017/S0021859696003759
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York. https://doi.org/10.1007/978-1-4757-2917-7_3
- CÁrcamo HA, Spence JR (1994) Crop type effects on the activity and distribution of ground beetles (Coleoptera: Carabidae). Environ Entomol 23(3):684–692. https://doi.org/10.1093/ee/23.3.684
- Chaplin-Kramer R, Megan E, Rourke O et al (2011) A metaanalysis of crop pest and natural enemy response to landscape complexity. Ecol Lett 14:922–932. https://doi.org/10.1111/j.1461-0248. 2011.01642.x



Chappell MJ, LaValle LA (2011) Food security and biodiversity: can we have both? An agroecological analysis. Agric Hum Values 28(1):3–26. https://doi.org/10.1007/s10460-009-9251-4

- Darvishi A, Yousefi M, Marull J (2020) Modelling landscape ecological assessments of land use and cover change scenarios. Application to the Bojnourd Metropolitan Area (NE Iran) Land Use Policy 99:105098. https://doi.org/10.1016/j.landusepol.2020.105098
- Darvishi A, Yousefi M, Dinan NM et al (2022) Assessing levels, tradeoffs and synergies of landscape services in the Iranian province of Qazvin: towards sustainable landscapes. Landsc Ecol 37:305–327. https://doi.org/10.1007/s10980-021-01337-0
- Dassou AG, Tixier P (2016) Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. Ecol Evol 6(4):1143–1153. https://doi.org/10.1002/ece3.1917
- Egger M, Smith GD, Schneider M, Minder C (1997) Bias in metaanalysis detected by a simple, graphical test. BMJ 315(7109):629–634. https://doi.org/10.1136/bmj.315.7109.629
- Feliciano D (2019) A review on the contribution of crop diversification to Sustainable Development Goal 1 "No poverty" in different world regions. Sustainable Dev 27(4):795–808. https://doi.org/10.1002/sd.1923
- Finch S, Collier RH (2000) Host-plant selection by insects—a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. Entomol Exp Appl 96(2):91–102. https://doi.org/10.1046/j.1570-7458.2000.00684.x
- Fischer-Kowalski M, Haas W, Wiedenhofer D, Krausmann F (2012) Socio-metabolic transitions during the 20th century and their impacts on the scale of human resource use. In: EGU General Assembly Conference Abstracts, p 9484. https://ui.adsabs.harva rd.edu/abs/2012EGUGA..14.9484F/abstract
- Gurr GM, Wratten SD, Landis DA, You M (2019) Habitat management to suppress pest populations: progress and prospects. Annu Rev Entomol 62(1):91–109. https://doi.org/10.1146/annurev-ento-031616-035050
- Habeck CW, Schultz AK (2015) Community-level impacts of white-tailed deer on understorey plants in North American forests: a meta-analysis. AoB PLANTS 7:119. https://doi.org/10.1093/aobpla/plv119
- Haddaway NR, Collins AM, Coughlin D, Kirk S (2015) The role of Google Scholar in evidence reviews and its applicability to grey literature searching. PLoS ONE 10(9):1–17. https://doi.org/10.1371/journal.pone.0138237
- Hatt S, Qingxuan X, Francis F, Chen J (2019) Intercropping oilseed rape with wheat and releasing *Harmonia axyridis* sex pheromone in Northern China failed to attract and support natural enemies of aphids. Biotechnol Agron Soc Environ 23(3):147–152. https:// doi.org/10.25518/1780-4507.17921
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecol 80(4):1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR] 2.0.CO:2
- Hooks CR, Johnson MW (2003) Impact of agricultural diversification on the insect community of cruciferous crops. Crop Prot 22(2):223–238. https://doi.org/10.1016/S0261-2194(02) 00172-2.
- Jones SK, Sánchez AC, Juventia SD, Estrada-Carmona N (2021) A global database of diversified farming effects on biodiversity and yield. Sci Data 8(1):1–6. https://doi.org/10.6084/m9.figshare. 14723913
- Kebede Y, Baudron F, Bianchi F, Tittonell P (2018) Unpacking the push-pull system: assessing the contribution of companion crops along a gradient of landscape complexity. Agric Ecosyst Environ 268:115–123. https://doi.org/10.1016/j.agee.2018.09.012
- Kleijn D, Bommarco R, Fijen TP et al (2019) Ecological intensification: bridging the gap between science and practice. Trends Ecol Evol 34:154–166. https://doi.org/10.1016/j.tree.2018.11.002

- Knörzer H, Grözinger H, Graeff-Hönninger S et al (2011) Integrating a simple shading algorithm into CERES-wheat and CERES-maize with particular regard to a changing microclimate within a relayintercropping system. Field Crops Res 121(2):274–285. https:// doi.org/10.1016/j.fcr.2010.12.016
- Koji S, Khan ZR, Midega CA (2007a) Field boundaries of Panicum maximum as a reservoir for predators and a sink for Chilo partellus. J Appl Entomol 131(3):186–196. https://doi.org/10.1111/j. 1439-0418.2006.01131.x
- Kremen C, Iles A, Bacon C (2012) Diversified farming systems: an agroecological, systems-based alternative to modern industrial agriculture. Ecol Soc 17(4):44. https://doi.org/10.5751/ES-05103-170444
- Lajeunesse MJ (2015) Bias and correction for the log response ratio in ecological meta-analysis. Ecol 96(8):2056–2063. https://doi.org/10.1890/14-2402.1
- Letourneau DK, Armbrecht I, Rivera BS et al (2011) Does plant diversity benefit agroecosystems? A Synthetic Review. Ecol Appl 21(1):9–21. https://doi.org/10.1890/09-2026.1
- Lin BB (2011) Resilience in agriculture through crop diversification: adaptive management for environmental change. Bioscience 61(3):183–193. https://doi.org/10.1525/bio.2011.61.3.4
- Lin L, Chu H, Murad MH et al (2018) Empirical comparison of publication bias tests in meta-analysis. J Gen Intern Med 33:1260–1267. https://doi.org/10.1007/s11606-018-4425-7
- Liu JL, Ren W, Zhao WZ, Li FR (2018) Cropping systems alter the biodiversity of ground-and soil-dwelling herbivorous and predatory arthropods in a desert agroecosystem: Implications for pest biocontrol. Agric Ecosyst Environ 266:109–121. https://doi.org/ 10.1016/j.agee.2018.07.023
- Lopes T, Bodson B, Francis F (2015) Associations of wheat with pea can reduce aphid infestations. Neotrop. Entomol 44(3):286–293. https://doi.org/10.1007/s13744-015-0282-9
- Lopes T, Hatt S, Xu Q et al (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
- Lu A, Gonthier DJ, Sciligo AR et al (2022) Changes in arthropod communities mediate the effects of landscape composition and farm management on pest control ecosystem services in organically managed strawberry crops. J Appl Ecol 59(2):585–597. https://doi.org/10.1111/1365-2664.14076
- Mansion-Vaquié A, Ferrer A, Ramon-Portugal F et al (2020) Intercropping impacts the host location behaviour and population growth of aphids. Entomol Exp Appl 168(1):41–52. https://doi.org/10.1111/eea.12848
- Marja R, Tscharntke T, Batáry P (2022) Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance a meta-analysis. Agric Ecosyst Environ 326:107822. https://doi.org/10.1016/j.agee.2021.107822
- McGurk E, Hynes S, Thorne F (2020) Participation in agri-environmental schemes: a contingent valuation study of farmers in Ireland. J Environ Manage 262:110243. https://doi.org/10.1016/j.jenvman.2020.110243
- Parajulee M, Slosser JE (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
- Parsons CK, Dixon PL, Colbo M (2007) Relay cropping cauliflower with lettuce as a means to manage first-generation cabbage maggot (Diptera: Anthomyiidae) and minimize cauliflower yield loss. J Econ Entomol 100(3):838–846. https://doi.org/10.1093/jee/100.3.838
- Poveda K, Kessler A (2012) New synthesis: plant volatiles as functional cues in intercropping systems. J Chem Ecol 38(11):1341–1341. https://doi.org/10.1007/s10886-012-0203-x
- Puliga GA, Arlotti D, Dauber J (2022) The effects of wheat-pea mixed intercropping on biocontrol potential of generalist predators in



- a long-term experimental trial. Ann Appl Biol 182(1):37–47. https://doi.org/10.1111/aab.12792
- Pustejovsky JE, Rodgers MA (2019) Testing for funnel plot asymmetry of standardized mean differences. Res Synth Methods 10(1):57–71. https://doi.org/10.1002/jrsm.1332
- R Development Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing: Vienna. https://www.R-project.org/
- Rohatgi A (2015) WebPlotDigitizer. Version 4.6. https://automeris.io/ WebPlotDigitizer. Accessed 9 Dec
- Root RB (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
- Rosa-Schleich J, Loos J, Mußhoff O, Tscharntke T (2019) Ecological-economic trade-offs of diversified farming systems–a review. Ecol Econ 160:251–263. https://doi.org/10.1016/j.ecolecon.2019.03.002
- Schütz L, Wenzel B, Rottstock T et al (2022) How to promote multifunctionality of vegetated strips in arable farming: a qualitative approach for Germany. Ecosphere 13(9):e4229. https://doi.org/ 10.1002/ecs2.4229
- Sinthumule NI (2023) Traditional ecological knowledge and its role in biodiversity conservation: a systematic review. Front Environ Sci 11:1164900. https://doi.org/10.3389/fenvs.2023.1164900
- Skelton LE, Barrett GW (2005) A comparison of conventional and alternative agroecosystems using alfalfa (Medicago sativa) and winter wheat (*Triticum aestivum*). Renew Agric Food Syst 20(1):38–47. https://doi.org/10.1079/RAF200478
- Smith HA, McSorley R (2000) Intercropping and pest management: a review of major concepts. Am Entomol 46(3):154–161. https:// doi.org/10.1093/ae/46.3.154
- Sterne JAC, Egger M (2005) Regression methods to detect publication and other bias in meta-analysis. In: Rothstein HR, Sutton AJ, Borenstein M (eds) Publication bias in metaanalysis: Prevention, Assessment, and Adjustments. Chichester, UK: John Wiley & Sons, pp 99–110. https://doi.org/10.1002/0470870168
- Tamburini G, Bommarco R, Wanger TC et al (2020) Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci Adv 6(45):eaba1715. https://doi.org/10.1126/sciadv.aba1715
- Tschumi M, Albrecht M, Collatz J et al (2016) Tailored flower strips promote natural enemy biodiversity and pest control in potato crop. J Appl Ecol 53:1169–1176. https://doi.org/10.1111/1365-2664.12653
- Varchola JM, Dunn JP (2001a) Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. Agric Ecosyst Environ 83(1–2):153–163. https://doi.org/10.1016/S0167-8809(00)00249-8
- Viechbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Sofw 36:1–48. https://doi.org/10.18637/jss.v036.i03
- Viechtbauer W, Viechtbauer MW (2015) Package 'metafor'. The Comprehensive R Archive Network. Package 'metafor'. http://cran.r-project.org/web/packages/metafor/metafor.pdf
- Yang Q, Li Z, Ouyang F et al (2022) Flower strips promote natural enemies, provide efficient aphid biocontrol, and reduce insecticide requirement in cotton crops. Entomol Gen 43:421–432. https:// doi.org/10.1127/entomologia/2022/1545
- Yousefi M, Darvishi A, Padró R et al (2020) An energy-landscape integrated analysis to evaluate agroecological scarcity. Sci Total Environ 739:139998. https://doi.org/10.1016/j.scitotenv.2020.139998
- Yousefi M, Darvishi A, Tello E et al (2021) Comparison of two biophysical indicators under different landscape complexity. Ecol Indic 124:107439. https://doi.org/10.1016/j.ecolind.2021.107439
- Zhou H, Chen L, Chen J et al (2013a) b) Adaptation of wheat-pea intercropping pattern in China to reduce *Sitobion avenae* (Hemiptera:

- Aphididae) occurrence by promoting natural enemies. Agroecol Sustain Food Syst 37(9):1001–1016. https://doi.org/10.1080/21683565.2013.763887
- Zhou HB, Chen JL, Yong LI et al (2013b) a) Influence of garlic intercropping or active emitted volatiles in releasers on aphid and related beneficial in wheat fields in China. J Integr Agric 12(3):467–473. https://doi.org/10.1016/S2095-3119(13)60247-6
- Zvereva EL, Kozlov MV (2021) Latitudinal gradient in the intensity of biotic interactions in terrestrial ecosystems: sources of variation and differences from the diversity gradient revealed by metaanalysis. Ecol Lett 24(11):2506–2520. https://doi.org/10.1111/ele. 13851
- Zvereva EL, Zverev V, Kozlov MV (2020) Predation and parasitism on herbivorous insects change in opposite directions in a latitudinal gradient crossing a boreal forest zone. J Anim Eco 89(12):2946– 2957. https://doi.org/10.1111/1365-2656.13350

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

References of the meta-analysis.

- 1.Agboka K, Gounou S, Tamo M (2006) The role of maize-legumes-cassava intercropping in the management of maize ear borers with special reference to Mussidia nigrivenella Ragonot (Lepidoptera: Pyralidae). InAnnales de la Société entomologique de France 42(3-4): 495-502. https://doi.org/10.1080/00379271.2006.10697484.
- 2.Belay D, Schulthess F, Omwega C (2009) The profitability of maize–haricot bean intercropping techniques to control maize stem borers under low pest densities in Ethiopia. Phytoparasitica. 37: 43-50. https://doi.org/10.1007/s12600-008-0002-7.
- 3.Denys C, Tscharntke T (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. Oecologia 130: 315-24. https://doi.org/10.1007/s004420100796.
- 4.Haenke S, Scheid B, Schaefer M, Tscharntke T, Thies C (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. Appl Ecol 46(5): 1106-14. https://doi.org/10.1111/j.1365-2664.2009.01685.x.
- 5.Hatt S, Lopes T, Boeraeve F, Chen J, Francis F (2017) Pest regulation and support of natural enemies in agriculture: experimental evidence of within field wildflower strips. Ecol Eng 98: 240-5. https://doi.org/10.1016/j.ecoleng.2016.10.080.
- 6.Hatt S, Qingxuan X, Francis F, Chen J (2019) Intercropping oilseed rape with wheat and releasing Harmonia axyridis sex pheromone in Northern China failed to attract and support natural enemies of aphids. Biotechnologie, Agronomie, Société et Environnement. https://doi.org/10.25518/1780-4507.17921.
- 7.Hummel JD, Dosdall LM, Clayton GW, Harker KN, O'donovan JT (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.
- 8.Jacques FL, Degrande PE, Gauer E, Malaquias JB, Scoton AM (2021) Intercropped Bt and non-Bt corn with ruzigrass (Urochloa ruziziensis) as a tool to resistance management of Spodoptera frugiperda (JE Smith, 1797)(Lepidoptera: Noctuidae). Pest Manag Sci 77(7): 3372-81. https://doi.org/10.1002/ps.6381.
- 9.Kebede Y, Baudron F, Bianchi F, Tittonell P (2018) Unpacking the push-pull system: Assessing the contribution of companion crops



along a gradient of landscape complexity. Agric Ecosyst Environ 268: 115-23. https://doi.org/10.1016/j.agee.2018.09.012.

- 10.Koh I, Holland JD (2015) Grassland plantings and landscape natural areas both influence insect natural enemies. Agric Ecosyst Environ 199: 190-9. https://doi.org/10.1016/j.agee.2014.09.007.
- 11.Koji S, Khan ZR, Midega CA (2007) Field boundaries of Panicum maximum as a reservoir for predators and a sink for Chilo partellus. J Appl Entomol 131(3): 186-96. https://doi.org/10.1111/j.1439-0418.2006.01131.x.
- 12.Lemke A, Poehling HM (2002) Sown weed strips in cereal fields: overwintering site and "source" habitat for Oedothorax apicatus (Blackwall) and Erigone atra (Blackwall)(Araneae: Erigonidae). Agric Ecosyst Environ 90(1): 67-80. https://doi.org/10.1016/S0167-8809(01)00173-6.
- 13.Liu J, Yan Y, Ali A, Wang N, Zhao Z, Yu M (2017) Effects of wheat-maize intercropping on population dynamics of wheat aphids and their natural enemies. Sustainability 9(8):1390. https://doi.org/10.3390/su9081390.
- 14.Lopes T, Bodson B, Francis F (2015) Associations of wheat with pea can reduce aphid infestations. Neotrop Entomol 44:286-93. https://doi.org/10.1007/s13744-015-0282-9.
- 15.Ludy C, Lang A (2006) A 3-year field-scale monitoring of foliage-dwelling spiders (Araneae) in transgenic Bt maize fields and adjacent field margins. Biol Control 38(3):314-24. https://doi.org/10.1016/j.biocontrol.2006.05.010.
- 16.Maluleke MH, Addo-Bediako A, Ayisi KK (2005) Influence of maize/lablab intercropping on lepidopterous stem borer infestation in maize. J Econ Entomol 98(2):384-8. https://doi.org/10.1093/jee/98.2.384.
- 17.Mansion-Vaquié A, Ferrante M, Cook SM, Pell JK, Lövei GL (2017) Manipulating field margins to increase predation intensity in fields of winter wheat (Triticum aestivum). J Appl Entomol 141(8): 600-11. https://doi.org/10.1111/jen.12385.
- 18.Mei Z, de Groot GA, Kleijn D, Dimmers W, van Gils S, Lammertsma D, van Kats R, Scheper J (2021) Flower availability drives effects of wildflower strips on ground-dwelling natural enemies and crop yield. Agric Ecosyst Environ 319:107570. https://doi.org/10.1016/j.agee.2021.107570.
- 19.Midega CA, Khan ZR, Van den Berg J, Ogol CK (2005) Habitat management and its impact on maize stemborer colonization and crop damage levels in Kenya and South Africa. African Entomology 13(2):333-40. https://hdl.handle.net/10520/EJC32643.
- 20.Midega CA, Khan ZR, Van den Berg J, Ogol CK (2008) Dippenaar-Schoeman AS, Pickett JA, Wadhams LJ. Response of ground-dwelling arthropods to a 'push–pull'habitat management system: spiders as an indicator group. J Appl Entomol 132(3): 248-54. https://doi.org/10.1111/j.1439-0418.2007.01260.x.
- 21.Midega CA, Khan ZR, Van den Berg J, Ogol CK, Bruce TJ, Pickett JA (2009) Non-target effects of the 'push-pull'habitat management

- strategy: parasitoid activity and soil fauna abundance. Crop Prot 28(12): 1045-51. https://doi.org/10.1016/j.cropro.2009.08.005.
- 22.Midega CA, Khan ZR, Van Den Berg J, Ogol CK, Pickett JA, Wadhams LJ (2006) Maize stemborer predator activity under 'push-pull'system and Bt-maize: a potential component in managing Bt resistance. Int J Pest Manag 52(1):1-0. https://doi.org/10.1080/09670870600558650.
- 23.Moore LC, Leslie AW, Hooks CR, Dively GP (2019) Can plantings of partridge pea (Chamaecrista fasciculata) enhance beneficial arthropod communities in neighboring soybeans?. Bio Control 128: 6-16. https://doi.org/10.1016/j.biocontrol.2018.09.008.
- 24.Ngangambe MH, Mwatawala MW (2020) Effects of entomopathogenic fungi (EPFs) and cropping systems on parasitoids of fall armyworm (Spodoptera frugiperda) on maize in eastern central, Tanzania. Biocontrol Sci Technol 30(5):418-30. https://doi.org/10.108 0/09583157.2020.1726878.
- 25.Pollier A, Tricault Y, Plantegenest M, Bischoff A (2019) Sowing of margin strips rich in floral resources improves herbivore control in adjacent crop fields. Agr Forest Entomol. 21(1): 119-29. https://doi.org/10.1111/afe.12318.
- 26.Ramsden MW, Menéndez R, Leather SR, Wäckers F (2015) Optimizing field margins for biocontrol services: the relative role of aphid abundance, annual floral resources, and overwinter habitat in enhancing aphid natural enemies. Agric Ecosyst Environ 199: 94-104. https://doi.org/10.1016/j.agee.2014.08.024.
- 27.Rischen T, Geisbüsch K, Ruppert D, Fischer K (2022) Farmland biodiversity: wildflower-sown islands within arable fields and grassy field margins both promote spider diversity. J Insect Conserv 26(3): 415-24. https://doi.org/10.1007/s10841-021-00363-2.
- 28. Schmidt-Entling MH, Döbeli J (2009) Sown wildflower areas to enhance spiders in arable fields. Agric Ecosyst Environ 133(1-2): 19-22. https://doi.org/10.1016/j.agee.2009.04.015.
- 29.Segre H, Segoli M, Carmel Y, Shwartz A (2020) Experimental evidence of multiple ecosystem services and disservices provided by ecological intensification in Mediterranean agro-ecosystems. J Appl Ecol 57(10): 2041-53. https://doi.org/10.1111/1365-2664.13713.
- 30.Skelton LE, Barrett GW (2005) A comparison of conventional and alternative agroecosystems using alfalfa (Medicago sativa) and winter wheat (Triticum aestivum). Renew Agric Food Syst 20(1): 38-47. https://doi.org/10.1079/RAF200478.
- 31. Tanyi CB, Nkongho RN, Okolle JN, Tening AS, Ngosong C (2020) Effect of intercropping beans with maize and botanical extract on fall armyworm (Spodoptera frugiperda) infestation. Int J Agron 26;2020. https://doi.org/10.1155/2020/4618190.
- 32. Török E, Zieger S, Rosenthal J, Földesi R, Gallé R, Tscharntke T, Batáry P (2021) Organic farming supports lower pest infestation, but fewer natural enemies than flower strips. J Appl Ecol 58(10): 2277-86. https://doi.org/10.1111/1365-2664.13946.



- 33.Tschumi M, Albrecht M, Bärtschi C, Collatz J, Entling MH, Jacot K (2016) Perennial, species-rich wildflower strips enhance pest control and crop yield. Agric Ecosyst Environ 220: 97-103. https://doi.org/10.1016/j.agee.2016.01.001.
- 34.Tschumi M, Albrecht M, Entling MH, Jacot K (2015) High effectiveness of tailored flower strips in reducing pests and crop plant damage. Proceedings of the Royal Society B: Biol Sci 282(1814): 20151369. https://doi.org/10.1098/rspb.2015.1369.
- 35. Varchola JM, Dunn JP (2001) Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. Agric Ecosyst Environ 83(1-2): 153-63. https://doi.org/10.1016/S0167-8809(00)00249-8.
- 36. Vernon RS, Kabaluk T, Behringer A (2000) Movement of Agriotes obscurus (Coleoptera: Elateridae) in strawberry (Rosaceae) plantings with wheat (Gramineae) as a trap crop. Can. Entomol 132(2): 231-41. https://doi.org/10.4039/Ent132231-2.
- 37. Wale M, Schulthess F, Kairu EW, Omwega CO (2007) Effect of cropping systems on cereal stemborers in the cool-wet and semi-arid ecozones of the Amhara region of Ethiopia. Agric For Entomol 9(2):73-84. https://doi.org/10.1111/j.1461-9563.2007.00324.x.
- 38.Wang G, Cui LL, Dong J, Francis F, Liu Y, Tooker J (2011) Combining intercropping with semiochemical releases: optimization of alternative control of Sitobion avenae in wheat crops in China. Entomologia Experimentalis et Applicata 140(3):189-95. https://doi.org/10.1111/j.1570-7458.2011.01150.x.

- 39.Woltz JM, Isaacs R, Landis DA (2012) Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. Agric Ecosyst Environ 152: 40-9. https://doi.org/10.1016/j.agee.2012.02.008.
- 40.Wu Y, Cai Q, Lin C, Chen Y, Li Y, Cheng X (2009) Responses of ground-dwelling spiders to four hedgerow species on sloped agricultural fields in Southwest China. Prog Nat Sci 19(3): 337-46. https://doi.org/10.1016/j.pnsc.2008.05.032.
- 41.Yang Q, Men X, Zhao W, Li C, Zhang Q, Cai Z, Ge F, Ouyang F (2021) Flower strips as a bridge habitat facilitate the movement of predatory beetles from wheat to maize crops. Pest Manag Sci 77(4): 1839-50. https://doi.org/10.1002/ps.6209.
- 42.Zhou H, Chen L, Chen J, Francis F, Haubruge E, Liu Y, Bragard C, Cheng D (2013) Adaptation of wheat-pea intercropping pattern in China to reduce Sitobion avenae (Hemiptera: Aphididae) occurrence by promoting natural enemies. Agroecol Sustain Food Syst 37(9): 1001-16. https://doi.org/10.1080/21683565.2013.763887.
- 43.Zhou HB, Chen JL, Yong LI, Francis F, Haubruge E, Bragard C, Sun JR, Cheng DF (2013) Influence of garlic intercropping or active emitted volatiles in releasers on aphid and related beneficial in wheat fields in China. J Integr Agric 12(3):467-73. https://doi.org/10.1016/S2095-3119(13)60247-6.

