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Diverse landscapes but not wildflower plantings increase marketable crop yield

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ABSTRACT

Biodiversity-friendly farming practices may create a win-win scenario for biodiversity and crop production by supporting ecosystem services to agriculture. On-farm wildflower plantings and conserving semi-natural habitat surrounding farms are two such practices that focus on the integration of non-crop components into production systems at the local and landscape scale, respectively. Here, we examine the impact of these practices on the regulating services of biological control and pollination, as well as the provisioning service of crop yield in four crops replicated across 22 farms in two US states. Wildflower plantings had no effect on pollination while their influence on pest control was both dependent on the landscape context and inconsistent across crops. In contrast, farms surrounded by higher amounts of semi-natural habitat had consistently higher marketable yields for all four crops. Our findings suggest a need to account for non-production values of wildflower plantings as they provide fewer direct production benefits than surrounding semi-natural habitats.

1. Introduction

Practices designed to support biodiversity and promote ecosystem services on agricultural land often aim to integrate non-crop habitat at local and landscape scales (Tscharntke et al., 2012). Wildflower plantings and landscape-scale semi-natural habitats around farms are generally believed to conserve beneficial organisms such as pollinators and natural enemies by providing nesting habitat, overwintering sites, supplemental food sources, and refuge from pesticides (Isaacs et al., 2009; Thies and Tscharntke, 1999). These beneficial organisms, in turn, are expected to enhance regulating services including pest control and pollination, and ultimately contribute to increased crop yields (Dainese et al., 2019). Enhancing these ecological relationships has the potential to meet the needs of farmers while maintaining the quality of the environment (Bommarco et al., 2013). While the effects of non-crop habitat on pest control and pollination have been studied extensively (Lichtenberg et al., 2017), their combined action and the ultimate impacts on crop yields remain understudied despite the clear importance to both farmers and policymakers (Chaplin-Kramer et al., 2019).

The potential for landscape-scale semi-natural habitat conservation or the creation of wildflower plantings to support crop yields may be limited by their ability to support multiple services simultaneously (Fig. 1). Recent syntheses suggest that on-farm wildflower plantings may be more likely than landscape-scale semi-natural habitat to enhance pest regulation services (Albrecht et al., 2020; Duarte et al., 2018; Karp et al., 2018), while the reverse is expected for pollination services (Albrecht et al., 2020; Kennedy et al., 2013; Lowe et al., 2021; Nicholson et al., 2020). Furthermore, the effectiveness of wildflower plantings may depend on the amount of semi-natural habitat in the broader landscape (Kleijn et al., 2011; Tscharntke et al., 2005), though empirical evidence for these context dependencies has been mixed (Albrecht et al., 2020; Grab et al., 2018). Our ability to resolve patterns of context-dependency and contrasting outcomes among regulating services remains limited by a lack of studies that measure both pest control and pollination services together in the same cropping system.

Similarly, in recent syntheses, only a fraction of included studies have included crop yield responses – 5% in (Holland et al., 2017); 34% in (Karp et al., 2018); 40% in (Albrecht et al., 2020) and 26% in (Lowe

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et al., 2021). Perhaps, for this reason, there is no consensus on the effect of landscape-scale semi-natural habitat or local wildflower plantings on crop yield. For example, Dainese et al. (2019) reported indirect positive effects of landscape-scale natural habitat on crop yield while Karp et al. (2018) found direct negative effects of natural habitat on yield. Even less frequently do studies report effects on crop quality or marketable yields, though these measures are more important to stakeholders (Chaplin-Kramer et al., 2019) and potentially more sensitive to variation in pests and pollinators than total yields (Classen et al., 2014; Garratt et al., 2014). In some cases, biodiversity-friendly farming practices may have negative effects on crop yield by increasing pest pressure (Tscharntke et al., 2016). Therefore, understanding the impacts that biodiversity conservation practices have on quality and yield across a range of crops will be critical for resolving these knowledge gaps.

We evaluated the effects of landscape-scale semi-natural cover and on-farm wildflower plantings on the regulating ecosystem services of pest control and pollination, and the provisioning ecosystem service of crop production using a hybrid experimental-observational approach. Our analyses focused on two unresolved questions: (1) does the value of local- and landscape-scale practices differ for pest control and pollination services; and (2) do local- and landscape-scale practices have consistent effects on yield across a range of crops?

2. Materials and methods

2.1. Experimental design

We selected 22 farms separated by > 2.5 km in the Mid-Atlantic region of the US spanning a semi-natural habitat gradient (10–70% at 1 km) and established wildflower plantings at 10 of these farms following recommendations of the USDA Natural Resources Conservation Service (Fig. S1). Semi-natural habitat cover (evergreen forest, deciduous forest, mixed forest, herbaceous wetlands, woody wetlands, and shrubland) was quantified at 250, 500, 1000-m radii around each farm based on the 2017 Cropland Data Layer (USDA-NASS, https://nassgeodata.gmu.edu/CropScape/). Wildflower plantings were established on 9 farms in the spring of 2016 and one farm in spring 2015. Wildflower plantings included a diverse mix of annuals and perennials, blooming continuously from early May–September with peak bloom occurring in late July (Angelella and O'Rourke, 2017). Details on farm location, characteristics, and wildflower mixes are described in Table S1 & S2 and (Angelella and O'Rourke, 2017).

At each farm, collards (*Brassica oleracea* var. Top Bunch), tomatoes (*Solanum lycopersicum* var. Defiant), strawberry (*Fragaria x ananassa* var. Chandler), and winter squash (*Cucurbita maxima* var. Gold Nugget) were grown in 190-litre plastic containers (Rubbermaid, Atlanta, GA). These crops represent spring and summer season crops that are commonly grown in the region. Growing crops in containers allowed for better control of abiotic factors that affected plant growth (Gibson, 2015). Drainage holes were drilled into the container bottoms. Containers were filled with Sun Gro soil (BFG, Burton, OH). Collards (5 plants per farm) and strawberries (6 plants) were grown at 20 farms both years. Tomatoes (2 plants) and squash (4 plants) were grown at 22 farms in 2017 and 19 farms in 2018. All crops were started in a greenhouse before being transplanted and were grown following common production practices for the region (Wyenandt et al., 2019). At farms with a wildflower planting, containers were placed approximately 2 m away from the planting.

2.2. Pest Control

Sentinel egg masses were used to quantify biological control in collards and tomatoes. Eggs of a common pest, cabbage looper, *Trichoplusia ni* (Hübner), were used on collards, whereas, brown marmorated stink bug, *Halyomorpha halys* (Stål), and corn earworm, *Helicoverpa zea* (Boddie) eggs were used on tomatoes. Four egg masses of each species were glued to wax paper and fastened to the bottom sides of leaves with paper clips in the field for 48 hrs twice per year. Biological control was measured as the proportion of damaged or missing eggs after exposure averaged across the season for each crop. Additionally, densities of the most abundant pests – imported cabbageworm, *Pieris rapae* L. and diamondback moth, *Plutella xylostella* L. – were recorded weekly on each collard plant. Similarly, yellowstriped armyworm, *Spodoptera ornithogalli* (Guenée) and hornworms, *Manduca* spp. (*M. sexta* L. and *M. quinquemaculata* Haworth) were recorded weekly for tomatoes. Pest counts were summed across the growing season for each plant for further analyses.

Pest damage was recorded in all four crops as the proportion of harvested items damaged by different pests. Leaf damage on collards caused by arthropods with chewing mouthparts was recorded. For tomatoes, piercing-sucking and chewing damage caused by arthropods to fruit were recorded. On strawberries we recorded damage including catfacing, soft spots, and cavities caused by *Lygus* spp., *Drosophila* spp., and sap beetles respectively. In squash, due to the sporadic nature of damage in the form of scars and blemishes caused by squash bug, *Anasa tristis* (DeGeer), and *Diabrotica* spp. beetles, their damage was quantified together.

2.3. Pollination

Pollination responses were collected for both strawberry and squash, which are considered moderately and highly pollinator-dependent, respectively (Klein et al., 2007), but not for collards and tomato which are considered pollinator independent (Klein et al., 2007). Strawberry bloom occurred in April and May earlier than the bloom period for the wildflower plantings while squash bloomed concurrent with the peak of

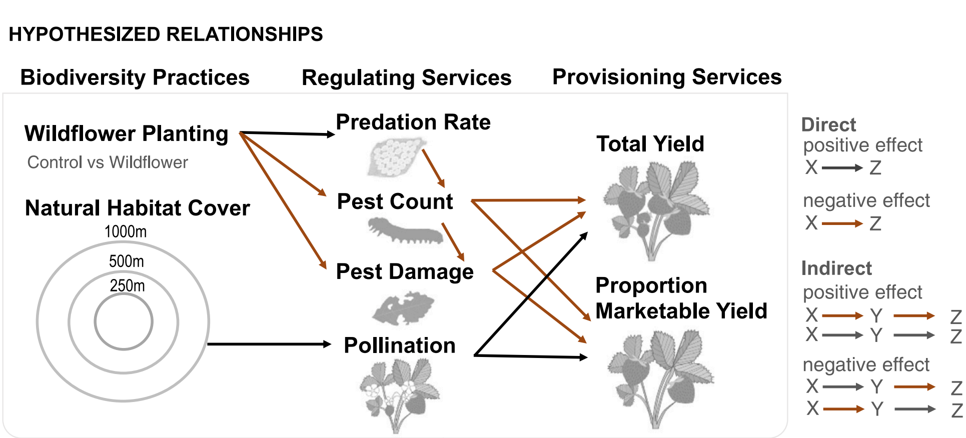

Fig. 1. Biodiversity-friendly farming practices such as establishing wildflower plantings and conserving semi-natural cover are expected to indirectly support the provisioning service of total and marketable crop yield through their expected benefits on the services of pest regulation and pollination. Hypothesized links are based on prior syntheses which found wildflower plantings to benefit pest regulation but not pollination, while landscape-scale semi-natural habitat benefits pollination but not pest regulation. Black lines indicate positive effects while red lines indicate negative effects.

flowering in the wildflower plantings. Pollination rate for strawberries was calculated as the number of fertilized achenes divided by total achenes per berry from a random subsample of all harvested berries per farm per year. Pollination rate in squash was quantified as the average number of seeds in mature, harvested squash from each farm per year.

2.4. Crop Yield

In all four crops, we used total and marketable yield counts as these units allowed us to discriminate between the quantity and quality of yield and represent common units of sale for these crops. Total yield for each crop was quantified as the total number of harvested fruits or leaves. For each crop, we graded harvested items following USDA guidelines (USDA-AMS, 2016, 2006, 1991, 1983). Marketable yield was then calculated as the number of grade 1 fruits or leaves divided by the total number of harvested fruit and leaves. By analyzing yield this way, we were able to standardize the production potential of each plant and reduce variability.

2.5. Statistical Analysis

To determine whether landscape or local biodiversity-friendly farming practices resulted in changes in regulating services and crop yield, we employed a structural equation modeling approach. This approach allowed us to explicitly model covariation between predictor variables and to evaluate direct and indirect effects of landscape and local practices on crop production. Separate path models were fit for each crop to accommodate differences among intermediate variable types for regulating services. The biodiversity practices of semi-natural habitat in the surrounding landscape and presence of a wildflower planting as well as their two-way interaction were included as exogenous predictor variables (not influenced by any other variable, Fig. 1). Response variables included the regulating services of pest regulation (egg predation, pest counts, pest damage) and pollination which were modeled as direct responses to the endogenous semi-natural habitat and wildflower planting predictors (Fig. 1). Direct links between egg predation and pest counts were included as well as direct links between pest counts and pest damage. For crops where multiple pests and their damage were recorded, these variables were included separately along with their correlated errors. Terminal response variables included the provisioning services of total and marketable yield which were modeled as a direct response of the exogenous biodiversity practices as well as indirectly mediated through pest counts, pest damage and pollination (Fig. 1).

Path models were constructed and evaluated using the `nlme` and `piecewiseSEM` packages (Lefcheck, 2016; Pinheiro et al., 2016). Pest counts were log-transformed to meet model assumptions. Correlated error terms were included among landscape scales, among counts for different pests, among types of crop damage, and between marketable yield and total yield. For each response variable, we included the presence or absence of a local wildflower planting and the proportion of semi-natural habitat at 250, 500, and 1000 m as well as their two-way interactions and upstream predictors (i.e., pest damage and pollination were included as yield predictors). Year was included as a fixed effect but was considered a nuisance variable. Random effects for each individual path included the nested terms of plant within farm to account for repeated measures. Hypothesized paths that were not statistically supported ($p > 0.1$) were removed from models by stepwise selection beginning with yield terminal responses and proceeding backwards. Finally, links identified as significant ($p < 0.05$) via tests of directed separation were added to the path set and the overall fit of each path model was assessed using the Fisher's chi-square distributed C-statistic (Shipley, 2009). Links between either pest counts or pest damage and crop yield measures were hypothesized to be negative indicating that increases in pests and pest damage were associated with reduced yields. However, positive links were occasionally detected which could indicate that farms with high yield were able to support higher pest densities or that farms which had very low yields had low pest density. In these cases, we also evaluated a model in which yield measures predicted pest measures and selected the model with the lowest Akaike Information Criterion score.

3. Results

3.1. Effects of landscape-scale semi-natural habitat on regulating services

Egg predation rates were not affected by semi-natural habitat cover in the surrounding landscape (Fig. 2, Tables S3-4) and high rates of egg predation were linked only to declines of imported cabbage worm counts in collards (std. estimate: −0.13, $P = 0.035$). Instead, we found that landscape-scale semi-natural habitat had direct but inconsistent effects on pest counts and pest damage across spatial scales. Though individual pest taxa exhibited variable responses to the landscape, greater semi-natural habitat at the 250 m scale led to consistent reductions in either pest counts or pest damage across crops (Fig. 2, Tables S3-6).

Pollination responses were similarly variable with respect to the landscape. In strawberry, semi-natural habitat at the 1000 m scale was associated with increased pollination rates (std. estimate: 0.23, $P = 0.036$) which in turn were linked to higher marketable yields (std. estimate: 0.20, $P = 0.002$). In squash, pollination was also an important driver of marketable yield (std. estimate: 0.24, $P = 0.014$) but was not impacted by semi-natural habitat cover in the surrounding landscape at any scale (Fig. 2; Table S6).

3.2. Effects of wildflower plantings on regulating services

Local-scale, on-farm wildflower plantings had variable effects on pest regulation among crops. Wildflower plantings had no effect on egg predation and did not affect pests in collards (Fig. 2; Table S3), but increased pest damage from *Drosophila* in strawberry (std. estimate: 0.20 $P = 0.047$; Fig. 2). In both tomato and squash, the effect of wildflower plantings on pest damage was mediated by the surrounding landscape (Fig. S2-3). There were no effects of wildflower plantings on pollination services in either strawberry or squash (Fig. 2).

3.3. Effects of semi-natural habitat and wildflower plantings on marketable and total yield

In all crops, we found links between regulating services and marketable yields but found few links with total crop yield (Fig. 2; Tables S3-6). In each crop, we found support for increased marketable yields that were indirectly linked to greater landscape-scale semi-natural habitat cover and wildflower plantings through their positive effects on pollination rates and pest regulation. In strawberries and squash where both pest control and pollination services were measured, we found that they displayed a roughly equal contribution to marketable yields (Fig. 2). Additionally, we found direct positive links between landscape-scale semi-natural habitat cover and marketable crop yields that were not explained by paths through pest regulation or pollination in three of the four crops (Fig. 2). In each case, a higher percent cover of semi-natural habitat surrounding farms at small to moderate spatial scales (250–500 m) was associated with direct increases in the proportion of marketable yields.

4. Discussion

Conserving and creating semi-natural habitat in working landscapes can provide biodiversity benefits, although it remains unclear whether these practices also provide crop production benefits (Karp et al., 2018; Nicholson et al., 2020). Despite inconsistent effects of semi-natural habitat on pest control and pollination, marketable yield was

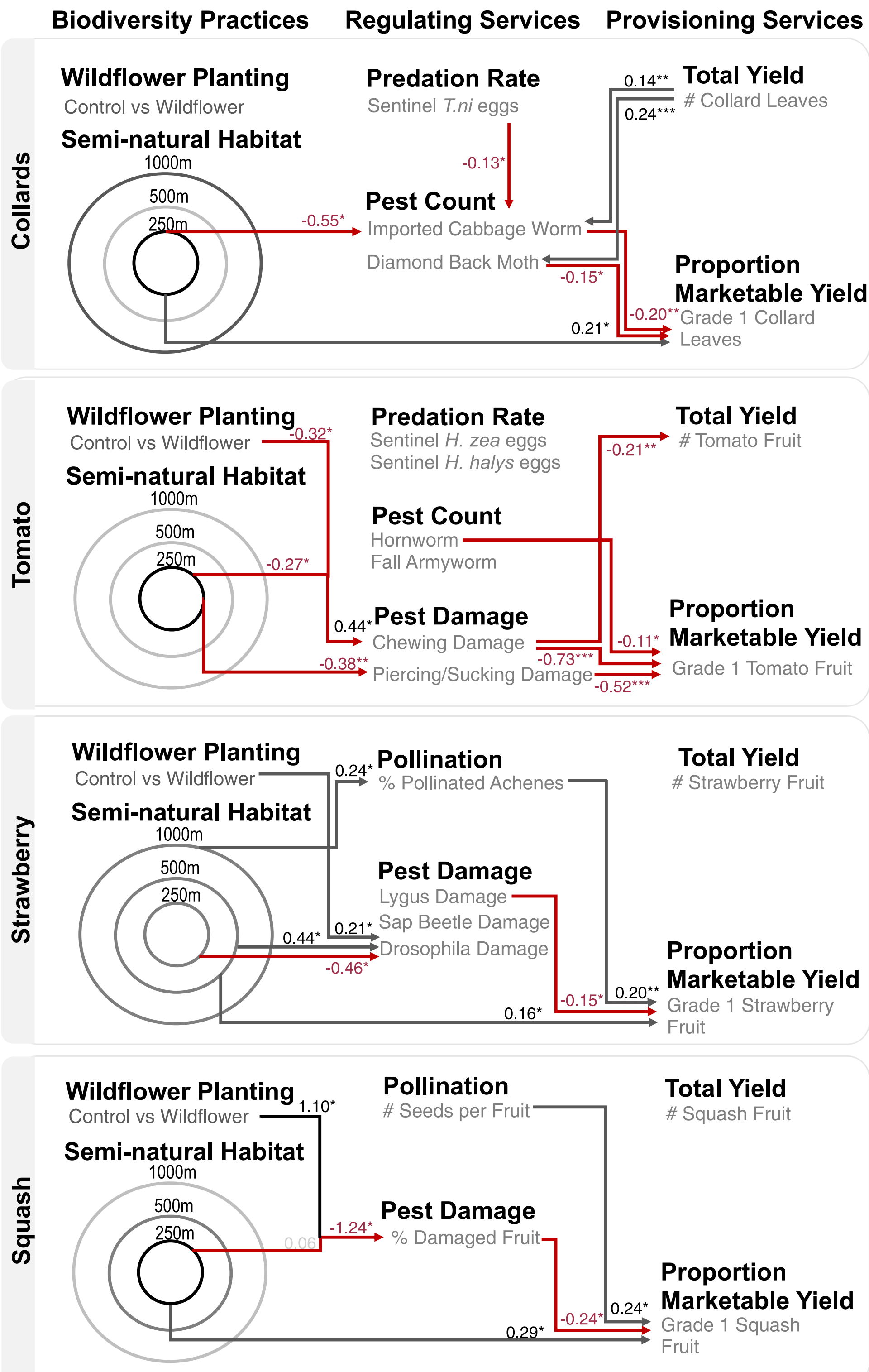

Fig. 2. Path diagrams representing the observed relationships between biodiversity-friendly farming practices (wildflower plantings and semi-natural habitat cover), regulating services (pest control and pollination), and provisioning services (total and marketable yield) in each of the four crops evaluated. Black paths indicate positive relationships while red paths indicate negative relationships. Non-significant paths and correlated errors not displayed. Standardized coefficients are given for each path. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

consistently higher on farms in landscapes with greater semi-natural cover. These findings suggest that landscape-scale semi-natural habitat, but not wildflower plantings, confers benefits for crop production across a range of crops.

Although semi-natural habitat at small to moderate spatial scales (250–500 m) was associated with reductions in pest counts or pest damage in all four crops, these effects were supported only for some pest groups and not others. Variation among taxa is likely responsible for the mixed patterns observed here and reported in Karp et al. (2018) and indicates that functional differences might explain variation in landscape responses (Martin et al., 2019; Tamburini et al., 2020). Similarly, differences in pollinator traits or even crop traits may explain the mixed effects of landscape-scale semi-natural cover on pollination services. Strawberry tends to be pollinated by a diverse community of largely generalist, wild bee species which are known to be susceptible to loss of semi-natural habitat within the landscape (Connelly et al., 2015). In contrast, squash is pollinated by a narrower community dominated by the honey bee, *Apis mellifera* L. and the squash specialist, *Eucera*

(Peponapis) pruinosa Say (Knapp and Osborne, 2019). These species, which are actively managed or dependent on agricultural habitats, are less impacted by semi-natural habitat in the surrounding landscape or even benefit from greater agricultural cover (Martin et al., 2019; McCullough et al., 2021). Additionally, strawberry requires more visits than squash to achieve full pollination (Chagnon et al., 1989; Tepedino, 1981) and produces lighter fruits when visited by honey bees than by native bees (MacInnis and Forrest, 2019). Compared to squash, pollination of strawberry may be more sensitive to changes in pollinator communities mediated by the landscape context, which may explain the pattern observed in our study.

In alignment with recent syntheses that have suggested few benefits of wildflower-rich plantings adjacent to crops for pollination (Albrecht et al., 2020), we found that pollination services were not impacted by wildflower plantings in either strawberry or squash. Data collected in the same system by Angelella et al. (2021) found no difference in the community composition of strawberry or squash pollinators between sites with and without a wildflower planting. Although wildflower plantings can increase pollinator diversity and abundance within restored areas (Nicholson et al., 2020) they may not provide sufficient resources to boost local pollinator populations to the point where they spillover into crop fields, at least not during the relatively short duration of most studies, including ours (Lowe et al., 2021). Our results also showed only mixed support for pest suppression benefits from wildflower plantings and that wildflower effects are mediated by landscape context in some instances. In some cases, wildflower plantings were even associated with increased damage to squash and strawberry. Because wildflower plantings frequently benefit pests, land managers will need to be vigilant if these pests also impact crop yields.

Yield measures have been poorly represented and syntheses drawing from many of the same source studies have reported contrasting outcomes (Dainese et al., 2019; Karp et al., 2018). By accounting for the indirect effects of semi-natural habitat on crop yields that can be explained by variation in pest control and pollination, we were able to detect both direct and indirect paths from semi-natural habitat to marketable yield in all four crops, while effects on total yield were inconsistent. In three quarters of crops, we observed direct positive effects of semi-natural habitat cover on marketable yield, suggesting that semi-natural habitat positively influences additional, unmeasured variables that influence yield. The species richness of the natural enemy and pollinator communities represent a likely unmeasured mediation variable, as a recent synthesis suggested that nearly 50% of the total loss in ecosystem services associated with landscape simplification could be attributed to richness reductions in service provider communities (Dainese et al., 2019). Crop quality measures stand out as important responses for future studies as they reflect the effects of management practices that integrate across multiple regulating services over the course of a growing season and represent an outcome ultimately valued by farmers.

5. Conclusions

The benefits to wildlife of integrating non-crop habitat on working lands are clear (Šálek et al., 2018) and we demonstrate that these practices provide additional benefits to crop production. We found that in the short term, conserving existing semi-natural habitat within the landscape is likely to result in greater benefits for crop production than creating smaller, flower-rich plantings adjacent to crops. Additionally, we found that pest and beneficial taxa frequently have idiosyncratic responses to management practices, which may obscure patterns when insect communities are measured in aggregate. Lastly, we highlighted the importance of testing the effects of management interventions on marketable yield which is both more responsive to variation in pest control and pollination and also more relevant for crop producers than total yields.

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CRediT authorship contribution statement

MO provided the conceptual framework. GA, CM, and JS established field sites and collected data. CM and HG performed the analyses and CM wrote the original draft of the manuscript and all authors contributed substantially to revisions.

Declaration of Competing Interest

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

Data Availability

All data and code supporting the results presented in the present version of the manuscript are available to editors and reviewers at: https://doi.org/10.7294/14531382.

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Conflicts of Interest

All authors declare no conflicts of interest related to the publication of this manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108120.

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