Ladybug landscapes: ecological and social dimensions of insect natural enemy conservation in Wisconsin agroecosystems

By

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Over the course of my PhD, I have often reflected on the absurdity of the conceit that a dissertation is a single-authored endeavor. The myth of the "lone genius" looms large in our cultural imagination of what a scientist is, but has never been accurate. Being a lone genius seems particularly implausible today, when the scale of science requires more time, skills, and brainpower than any individual possesses (not to mention the logistical, social, and emotional supports that make it possible). Even if producing excellent research all on my own were possible, I wouldn't choose it; doing science with others is too much fun.

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Abstract

The simplification of crop fields, farms, and agricultural landscapes is associated with decreased biodiversity and ecosystem services, such as natural pest control provided by arthropod natural enemies. While diversification may improve conservation and pest control outcomes in some cases, ecological predictions are often weak and habitat management at large spatial scales remains an unpopular strategy for agriculture. This dissertation seeks to address these agroecological challenges through multidisciplinary research that investigates the relationships among insects, crops, landscapes and people in southern Wisconsin, USA, with a particular focus on predatory lady beetles (Coccinellidae). In the first chapter, I empirically test the prediction that landscapes with more abundant, stable prey resources support larger predator populations with a landscape-scale mensurative experiment in two study years. My results confirm the close association of lady beetles with semi-natural habitat, but do not provide evidence that adult lady beetle population sizes are influenced by spatio-temporal patterns of aphids in the landscape. A possible explanation for why I did not observe this hypothesized relationship is that aphids alone do not adequately capture the full diversity of resources utilized by lady beetles in heterogenous landscapes. Landscape supplementation—the process by which consumers benefit from substitutable resources from multiple adjacent habitats—could be an important mechanism for lady beetle persistence, but empirical evidence is lacking. My second chapter thus employs a DNA metabarcoding approach to investigate how the presence and taxonomic richness of arthropod prey in lady beetle diets vary by local habitat and landscape structure. Lady beetles communities in more diverse, cropped landscapes were associated with greater prey detection rates and prey taxa richness. Our results suggest that the realized diet breadth of wild lady beetles may be under-appreciated, and increasing the diversity of crop and non-crop habitats in a landscape may be an especially effective conservation strategy for mobile generalists. This work demonstrates that landscape-scale processes are consequential for natural enemies and biological control, but farmers do not typically have the ability to shape or decide their landscape context. Accordingly, my third chapter investigates the potential for temporally diversifying crops at the field-scale to enhance pest suppression. In a three year experiment, I compared aphids and predators in monocultures of early-season small grain crops and late-season soybeans to polycultures that contained temporally complementary crops in the same plot. I find that larger predator communities earlier in the growing season were associated with lower aphid population growth rates in soybean, but the impact of diversification on these dynamics was inconsistent, possibly because treatment differences were obscured by larger-scale processes. The substantial influence of landscape structure on conservation biocontrol outcomes underscores the importance of social processes in shaping agro-environmental outcomes. It is these processes to which I turn my attention in the fourth chapter, which draws from rural sociology, political ecology, and science and technology studies to analyze institutional constraints on the adoption ecological insect and landscape management practices by Wisconsin farmers. Overall, this dissertation illuminates pathways for the ecological intensification of agriculture and the adoption of alternative insect management paradigms. It identifies landscape-scale processes as integral components of more sustainable farming, making pest control and biodiversity conservation collective problems that require coordination among multiple stakeholders. To slow agricultural drivers of insect declines, large-scale coordination and political-economic change may be necessary. My findings contribute to the understanding of the socio-ecological complexities of insect natural enemy conservation in agricultural landscapes, and provide insights for the continued development of ecological intensification schemes.

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Introduction

Insect apocalypse now

Where have all the insects gone? This question has been bugging scientists in recent decades as evidence accumulates that something is going terribly wrong for those "little things that run the world" (Wilson 1987). Sometime in the early 2000s, entomologists in the United Kingdom began wondering about the absence of once-abundant insect corpses splattered across windshields after long summer car rides. Researchers were trying to develop an easy way to measure baseline rates of insect biomass over large geographic areas, resulting in several novelty news articles about "splatometers," sticky plastic rectangles that could be attached to car license plates (McCarthy 2004). Although splatometer studies seem not to have caught on, renewed scientific and public interest in the "windshield phenomenon" came in October 2017 when a collection of academics and members of a small German entomological society published a paper with a flashy finding: over the course of three decades, insect biomass had declined by more than 75% across dozens of protected areas within the western part of the country (Hallmann et al. 2017).

Almost exactly one year later, insect declines were reported from forests in Puerto Rico, with cascading consequences for the lizards, frogs and birds that depended on those insects for food (Lister and Garcia 2018). Popular outlets like the *New York Times* and the *Guardian* picked up these stories, characterizing them as harbingers of an "insect apocalypse." One scientific literature review went so far as to project that "insects as a whole will go down the path of extinction in a few decades" (Sánchez-Bayo & Wyckhuys 2019). While this hyperbolic claim is not well supported—the same article showed that we know remarkably little about long-term trends for most insect populations globally—it does not mean alarm is unfounded. Multiple lines of evidence suggest the threat of insect declines is real and pressing for human and non-human ecologies, and the patchy knowledge we do have is sufficient for action (Forister et al. 2019).

One of the primary culprits implicated in this Armageddon is modern agriculture (Wagner 2020; Goulson 2021). The insect and land management practices that have contributed to the current state of affairs are components of an industrial syndrome of production (Vandermeer 1997; Vandermeer and Perfecto 2012) whereby production factors that were once largely generated on-farm are increasingly substituted with off-farm inputs. These include replacement of human and animal knowledge and labor with machines and proprietary digital technologies (Olmstead and Rhode 2001; Miles 2019; Carolan 2020); locally bred and adapted seeds with commercial hybrid and engineered varieties (Lewontin and States 1986; Kloppenburg 2005; Montenegro de Wit 2017); crop residues, manure, and other organic waste with synthetic fertilizers (Foster 1999); and endogenous cultural and biological pest controls with purchased chemical biocides (Russell 2001; Nicholson and Williams 2021). In general, the industrial syndrome tends towards standardization and simplification, often coming into conflict with messy ecological realities (Vandermeer and Perfecto 2012; Guthman 2019).

Simple landscapes, difficult problems

This simplification is evident on the landscapes. With industrialization, farming regions have become increasingly homogenous—large areas of monocropped fields (White and Roy 2015), low levels of planned and associated agrobiodiversity (Jackson et al. 2007; Aguilar et al. 2015; Crossley et al. 2020), and little retention of natural, semi-natural, or other non-crop vegetation (Lark et al. 2020). Such landscapes are often associated with reductions in the abundance and/or diversity of natural enemies of crop pests (Letourneau et al. 2011; Chaplin-Kramer et al. 2011; Dassou and Tixier 2016; Dainese et al. 2019), and replacement of natural pest suppression with increased rates of pesticide application (Meehan et al. 2011; Meehan and Gratton 2015; Paredes et al. 2020; Larsen and Noack 2021; Gagic et al. 2021; Nicholson and Williams 2021). This is consequential not only for agriculture, but also public health and environmental justice (Harrison 2011; Bourguet and Guillemaud 2016; Nicolopoulou-Stamati et al. 2016).

While agroecosystem diversity in general tends to promote natural enemies and impede pests, this is by no means a guarantee (Tscharntke et al. 2016; Karp et al. 2018). One reason for this may be that diversity per se is not necessarily beneficial if it is not supplementing otherwise limiting resources. For example, “natural habitat” around farm fields is typically assumed to provide food and shelter for natural enemies, but actual resources are rarely measured directly. When they are, there tends to be substantial local heterogeneity in the quantity and quality of resources that semi-natural habitat provides (Sarthou et al. 2014; Holland et al. 2016; Bartual et al. 2019).

A related issue is that the timing of resources availability is infrequently considered when evaluating a landscape's conservation potential. Diverse vegetation may be most beneficial to natural enemies when plant species have asynchronous phenologies, creating a pattern of season-long resource complementation (Schellhorn et al. 2015; Iuliano and Gratton 2020). Empirical evaluations of this hypothesis in the conservation biological control literature is scant, but could substantially contribute to ecological understanding of pest and enemy dynamics and inform the design of more sustainable cropping systems.

Finally, conservation biological control is limited not only by ecological knowledge, but also social, economic, and political forces (MacIntyre 1987; Palladino 1996; Chaplin-Kramer et al. 2019). Overcoming these limitations requires integrating the study of people's relationships with their environment and non-human beings into research on biodiversity and ecosystem services in agricultural landscapes.

Dissertation outline

To address these agroecological knowledge gaps, I conducted a multi-disciplinary study of the relationships among some of the insects, crops, landscapes, and people that coincide in Southern Wisconsin. In a landscape-level study, I surveyed agricultural fields and adjacent non-crop habitats at study sites selected along a novel resource continuity gradient to evaluate the influence of spatio-temporal patterns of aphids on communities of predatory lady beetles (Chapter 1). Across this gradient, I also collected beetles for diet evaluation using DNA metabarcoding and Next Generation Sequencing (NGS) to understand the drivers of lady beetle foraging patterns in these landscapes (Chapter 2) To evaluate how resource continuity affects insect population dynamics in more controlled conditions, I designed a field-level experiment to test whether and in what configuration the planting of phenologically complementary crops can bolster pest control by generalist predators (Chapter 3). Finally, I conducted qualitative interviews with Wisconsin farmers who span a gradient of production systems and landscape contexts to understand how environmental, social, economic, and political forces shape insect management paradigms and landscape structure (Chapter 4). This research advances both basic and applied knowledge of landscape agroecology, predator-prey interactions, and human-nature relationships.

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Chapter 1

Semi-natural habitat, but not aphid amount or continuity, predicts lady beetle abundance across agricultural landscapes

Abstract

The amount of semi-natural habitat surrounding farm fields is a common but inconsistent predictor of natural enemy populations and pest suppression. Standard landcover metrics may not accurately capture the actual availability of limiting resources for natural enemies and can miss important resource dynamics across space and time. Theory from animal movement and landscape ecology predicts that regions with more, spatio-temporally continuous resources should have larger predator populations enhanced biological control. To test these predictions empirically, we designed a study measuring aphids, lady beetles, and predation services across agricultural landscapes in Wisconsin, USA. Across two study years we sampled lady beetles and aphids in 336 crop fields and adjacent semi-natural habitat patches at 5–7 time points each, and in one year we assessed predation with sentinel egg cards. We used aphid counts to model landcover-specific prey phenologies, from which we calculated novel landscape indices of prey amount and continuity. These indices, along with semi-natural habitat area, were then used to predict lady beetle abundance. Results show that while there were strong differences in the abundance and timing of aphids by landcover, semi-natural habitat was still a better predictor of lady beetle counts and sentinel egg predation than either aphid amount or continuity indices. Our findings confirm the robust relationship between lady beetles and semi-natural habitat in agricultural landscapes, and highlight the complexities of measuring fine-scale heterogeneity in real landscapes. Future work should continue to refine experimental methods for the successful integration of landscape ecology and animal behavior to support conservation goals.

Author contributions Ben Iuliano, Claudio Gratton, Tania Kim, and Brian Spiesman conceived of and designed the study. Ben Iuliano led field work, data analysis, and wrote the first manuscript draft. Claudio Gratton reviewed and contributed to subsequent drafts.

Introduction

Conventional wisdom of conservation biological control holds that more complex landscapes—typically defined as those with a greater proportion of (semi-)natural habitat surrounding farm fields—support more abundant and diverse predator communities, resulting in enhanced natural pest suppression, reduced need for chemical pesticides, and (in some cases) greater yields (Corbett and Rosenheim 1996, Marino and Landis 1996, Thies and Tscharntke 1999, Landis et al. 2000). While numerous field studies (Rusch et al. 2013, Paredes et al. 2019, Perez-Alvarez et al. 2019), large-scale data analyses (Meehan et al. 2011, Paredes et al. 2020, Gagic et al. 2021), and literature syntheses (Bianchi et al. 2006, Rusch et al. 2010, Chaplin-Kramer et al. 2011, Martin et al. 2019, Dainese et al. 2019) have found support for this hypothesis, others have called its generalizability into question (Karp et al. 2018).

Several explanations have been proposed for these inconsistent results (Tscharntke et al. 2016). One idea is that classification of "natural habitat" and "cropland" may be too coarse to effectively capture resource patterns that natural enemies respond to in agricultural landscapes (Vasseur et al. 2013). Differences in plant species, vegetation structure, management practices, etc. in each of these categories are highly variable, and lumping together all "natural" and "cropped" habitats obscures these differences which can have important consequences for organisms and their interactions. Directly evaluating limiting resources, such as food and shelter, in different habitat types could offer a more reliable and mechanistic approach for predicting which landscapes will support abundant natural enemy populations and improve pest suppression.

In addition to the spatial considerations associated with classifying habitats in a landscape, temporal variation in resources is likely important for insect populations but infrequently taken into account in CBC studies (Iuliano and Gratton 2020). Many natural enemies are long-lived, highly mobile, and able to take advantage of resources in different habitats over the course of their lifecycle. Thus, a static perspective of the value of particular landscape elements to natural enemies is likely insufficient to predict their occurrence and services. Synthesizing approaches from animal movement and landscape ecology to study resource tracking could be a fruitful avenue for more predictive CBC research and management. Specifically, mobile consumers such as natural enemies are likely to benefit or suffer from particular patterns of resource abundance, timing, ephemerality, and predictability over large spatial extents (Abrahms et al. 2021).

Temporal resource patterns are increasingly viewed as an important dimension of agroecosystem heterogeneity (Welch and Harwood 2014, Cohen and Crowder 2017). One prediction emerging from a temporal perspective is that a dearth of resources during particular parts of the season could be a factor limiting the persistence and abundance of natural enemies. As such, it has been suggested that planting phenologically complementary crops could "link the resource chain" for mobile predators and bolster their populations, by approximating the conditions of perennial habitats. While this hypothesis is conceptually appealing and has some theoretical support (Schellhorn et al. 2015, Spiesman et al. 2020), empirical evidence is sparse, particularly at the landscape scale.

In this study we investigated how prey resource patterns in agricultural landscapes affect the abundance of a dominant predatory insect taxon, aphidophagous lady beetles (Coleoptera: Coccinellidae). Specifically, we sampled lady beetles and their aphid prey at a high spatial and temporal resolution to ask whether the landscape-scale amount and continuity of aphid prey better predicts lady beetle abundance than landcover alone. While different lady beetle species can vary in habitat and diet breadth, most in our region require aphids to fully develop, and in many cases their populations are tightly coupled to aphid densities (Donaldson et al. 2007, Bahlai et al. 2015b, Pan et al. 2020). Lady beetles are also relative generalists , feeding on multiple aphid species that occur across different crop and non-crop habitats (Lundgren 2009, Hodek and Evans 2012). Thus, they are a useful group with which to test questions about spatio-temporal resource patterns in heterogeneous landscapes. We hypothesized (1) that different crop and non-crop habitats offer distinct phenological patterns of aphid prey, creating the opportunity to test how temporal variation in food resources influence mobile predators at the landscape scale. We therefore hypothesized (2) that resource-based landscape quantifications, both in the amount and continuity of aphid prey, would better predict (a) lady beetle abundance and (b) predation services than the proportion semi-natural habitat in the surrounding area.

Methods

Study system and site selection

This research was conducted in southern Wisconsin, USA. The region is highly agricultural and is characterized by a mosaic of small to medium-sized farms with annual crop rotations covering most of the landscape (corn, soybean, alfalfa, and small grains, >50% of agricultural land; USDA NASS 2021). Natural and semi-natural habitat patches are also common in these landscapes, including pastures, wetlands, deciduous woodlands, and conservation grasslands/prairies. Landscape composition spans a range of land cover (and thus potentially phenological) diversity, making this a suitable region in which to explore how variation in landcover and resource availability influences insect natural enemies.

We selected 17 landscapes (defined as contiguous areas within 1.5 km circular buffers) in two study years (2019 and 2021) in which to conduct insect surveys, 10 landscapes of which were sampled in both years of the study (Figure 1.1). In 2019, landscapes were selected along a gradient of expected variation in the total amount and temporal continuity of aphid prey. This was determined using literature review of crop pest phenology for the state (e.g. Jensen and Smith n.d.) and data from the Midwest Aphid Suction Trap Network (Lagos-Kutz et al. 2020). Briefly, we assigned scores based on the expected relative abundance of aphids in different landcover types at different time points (early-, mid- and late-season). We then used these relative scores to calculate the expected total (season-long) amount, patch-level temporal variance, and landscape-level temporal variance of relative aphids abundance in 1,000 randomly selected landscapes across the study region. Based on this analysis, we chose

17 landscapes that spanned the range of our two primary resource gradients (total amount and temporal variability in amount of prey) while considering logistical sampling constraints (e.g. driving distances, land owner contacts). In 2021, we used our data and experience from 2019 to inform the selection of 7 new landscapes.

In contrast to the more common "focal field" approach used in landscape pest control studies (Gardiner et al. 2009a, Liere et al. 2015), we employed a "whole landscape" approach to test our hypotheses. Rather than sampling a single patch of the same habitat type in each landscape (e.g., predator and prey abundance within one soybean field), we surveyed 8-10 different habitat patches in the landscape in proportion to their cover within the 1.5 km buffer (Figure 1.1). We used the USDA Cropland Data Layer classification (USDA NASS) available for each year of the study, reclassified to the six most common vegetative land covers in the region to represent the habitat patches for sampling: corn, soybean, alfalfa, small grains, grassland/pasture, and woodland. We avoided sampling in regions dominated by other land uses (e.g. water, urban areas) because of their relative uncommonness and low resource potential for aphids and lady beetles.

Field surveys

At each habitat patch, we conducted insect surveys at approximately 3 week intervals over the course of the growing season. In 2019, each habitat patch was sampled 4-5 times between June and September; in 2021 each patch was sampled 6-7 times between May and

October. At each visit we established an area approximately 10x30m within a particular habitat patch at least 5 m from a patch edge from which to sample insects using sweep nets, vegetation beating, and yellow sticky cards.

Sweep nets and vegetation beating were employed to sample aphids, which were identified to superfamily Aphidoidea and counted. To sample herbaceous ground cover vegetation, we conducted four sets of 25 back-and-forth sweep samples using a standard (38 cm diameter) canvas sweep net (BioQuip, Rancho Dominguez, CA) in a "W" pattern across the sampling area. After each set, bag contents were emptied into a white plastic dishpan (40 cm x 32 cm x 15 cm) for identification and counting in the field. If aphids exceeded 100 individuals per sample, we subsampled counts from one quarter of the dishpan and extrapolated to the full sample. In habitats with tall, woody vegetation (e.g forest patches, woodlots) we also conducted branch beating in order to account for resource availability in the understory (due to logistical constraints, we were unable to survey insects in the canopy). Paralleling sweep samples, we beat four sets of 10 branches into white plastic dishpans, identifying and counting the contents of the dishpan after each set. Aphid counts from both methods were summed for analysis.

We surveyed adult aphidophagous lady beetles at each patch using two yellow sticky cards (Great Lakes IPM, Vestaburg, MI; Trécé PHEROCON AM no-bait traps or Scentry Multigard traps) mounted ~1.5 m off the ground on green plexiglass gardening stakes. While sticky cards have limitations, they are a robust and common method for measuring relative differences in lady beetles across habitat types (Parajulee and Slosser 2003, Gardiner et al. 2009b, Bahlai et al. 2013). Sticky cards were collected and replaced with fresh cards upon each visit. Upon collection cards were covered with transparent acetate sheets and stored in a −20 °C freezer until insects could be identified and counted in the lab. Lady beetles were identified to species with the exception of the spurleg lady beetles (Brachiacantha spp.), which were identified to genus due to species-level classification discrepancies among observers.

This sampling scheme resulted in two hierarchical datasets: 1) aphid counts in sweep net/branch beating samples from 2,007 patch-dates, and 2) lady beetle counts on 3,209 sticky cards from 1,635 patch-dates, grouped into 17 landscapes in two study years.

Sentinel prey experiment

In 2021, we conducted a sentinel prey assay to measure how predation services varied between habitat types and across landscape gradients. Following Werling et al. (2011), we constructed egg cards using freezer-killed corn rootworm (*Helicoverpa zea*) eggs (Benzon Research, Carlisle, PA). Sections of muslin cloth containing 50-70 eggs were cut out and glued onto green 3x5 in index cards. Cards were examined under a light microscope to count the total number of eggs and initial number of damaged eggs.

During the fourth sampling round (July 12 to July 28 2021) we placed two uncovered egg cards at each patch in 17 sampling landscapes. Previous experience has shown loss of eggs due to causes other than predation, as measured by the inclusion of covered "control" cards, is negligible (Werling et al. 2011); thus, all cards in this experiment were left uncovered and available to predators. Cards were fixed with binder clips to the underside of the leaves of dominant vegetation, or in a few cases to green gardening stakes where this was not possible. Egg cards were retrieved approximately 24 hours later, at which time they were brought back to the lab and again counted for total and damaged eggs. Damage was defined as eggs missing >50% of their original mass or with clear signs of consumption from piercing/sucking insects. Predation was quantified as the number of eggs removed plus the number of damaged eggs minus the number of initial damaged eggs. This experiment resulted in a dataset of predation values for 300 recovered egg cards from 154 patches in one study year.

Statistical analyses

All statistical analyses were conducted in R (R Core Team 2023) and RStudio version 2022.12.0+353 (RStudio Team 2023). Model diagnostics were assessed using the DHARMa package (Hartig and Lohse 2022) and contrasts were constructed with emmeans (Lenth et al. 2023). Results were visualized with ggeffects (Lüdecke et al. 2023), visreg (Breheny and Burchett 2020), and ggplot2 (Wickham 2016) packages. Landscape variables were calculated using the landscapemetrics package (Hesselbarth et al. 2022) with a buffer of 1.5km around the centroid of sampling patches in each landscape, as this is the extent within which samplings patches were designated within landscapes, and is consistent with other ecological studies on Coccinellids (Gardiner et al. 2009b, Woltz and Landis 2014, Tiede et al. 2022).

To compare aphid phenology across different habitat types (Hypothesis 1), we used the mgcv package (Wood 2023) to construct a generalized additive mixed model (GAMM) for the number of aphids observed as a function of calendar day and its interaction with habitat as the smooth term, with a negative binomial distribution and log link. To account for variation in aphid populations between sampling years, we also included year and its interaction with habitat as fixed parametric terms in the model, and sampling location within year as a random effect.

We then used modeled aphid phenology curves to calculate indices of landscape-scale aphid amount and continuity. Briefly, for each landscape-year, the proportion of each habitat in a given landscape was weighted by the modeled habitat-specific aphid abundance over the course of the growing season (Figure S1.1). We calculated an index for total landscape-scale aphid availability as the area under the landscape-specific phenology curve. As an index of landscape-scale aphid continuity, we used the residuals of the correlation between the mean and variance of aphids over time (to account for increasing variance with higher mean abundance). We multiplied these values by −1, so that more negative values correspond to greater temporal variation (i.e. less continuity) and more positive values correspond to smaller temporal variation (i.e. more continuity). Both indices were transformed to z-scores for use as predictor variables in models constructed for testing Hypothesis 2. Using raw aphid counts for each landscape to construct amount and continuity indices did not qualitatively change results (data not shown).

To test the effects of landscape-scale prey indices and semi-natural habitat area on lady beetle abundance (Hypothesis 2a), we constructed generalized linear mixed effects models with a Poisson distribution and log link using the glmmTMB package (Brooks et al. 2022). We modeled lady beetle counts from sticky cards in each landscape as a function of local habitat type, semi-natural habitat cover in the landscape, landscape-scale aphid availability, and landscape-scale aphid continuity. Due to differences in the sampling period and duration between years, we modeled data from 2019 and 2021 separately. In 2019, there was strong collinearity between semi-natural habitat and our continuity metric (Pearson's r = 0.7; Figure S1.2), so we fit reduced models with these terms separately. Sticky cards were occasionally knocked over or missing from sampling locations, resulting in lower sampling effort at some patches. To account for this, we used the total trap number per patch as an offset term in models. To account for non-independence of samples from the same landscape, we included a random intercept for landscape, and we included an observation level random effect to control overdispersion in the data (Harrison 2014).

To test the effect of landscape predictors on predation (Hypothesis 2b), we constructed a generalized linear mixed effects model with a binomial distribution and logit link using the glmmTMB package. The model included habitat and its interaction with natural habitat, prey amount, and prey continuity, with random intercepts for patch ID and landscape to account for non-independence and an observation-level random intercept to control overdispersion. Because we were interested in the overall effect of semi-natural habitat regardless of local habitat, we implemented weighted effects coding using the wec package (Nieuwenhuis et al. 2017). In weighted effects coding, the effect of each category (here, local habitat) represents the deviation of that category from the sample mean (te Grotenhuis et al. 2017). This allowed us to test if there was an overall effect of landscape on predation across all local habitat types, as well as if there are any habitats for which the relationship between predation and landscape is statistically different from the general trend.

Results

Effect of habitat on aphid phenology

Across the two sampling years, we counted 72,749 aphids across 1,987 surveys. GAMM results showed strong evidence for differences in both the total amount and phenological pattern of aphids across the six habitat types sampled. On average, aphid counts in alfalfa (121.37 ± 35.94 aphids per sample) were greater than counts in other habitats by two orders of magnitude. The habitat with the next highest aphid counts was grassland, small grains, soybeans, woodlands, and corn (Figure S1.4, Table S1.1).

There was strong evidence of different patterns of aphid abundance over the growing season in different habitat types (all *p*-values for habitat by date smooth terms <0.001; Figure 1.2). Perennial habitats of alfalfa, grasslands, and woodlands had relatively stable aphid abundance (with a slight decrease in the middle of the season). Aphid populations in annual crops (small grains, soybean, corn) were more ephemeral: in small grains (wheat, oats, rye) aphid abundance peaked in early June and declined over the rest of the season, while in corn and soybean aphids were relatively absent until late July, after which time they increased through the end of the sampling period. There was strong evidence that aphid counts were about three times higher in 2019 than in 2021 for corn and grassland habitats, and about ten times higher in soybean (all *p*-values <0.01); for alfalfa, small grains, and woodland habitats, there was no statistical difference between years (Figure S1.4, Table S1).

Landscape-level predictors of lady beetle abundance

Across all sticky cards, we collected 3,759 lady beetles from 15 species. We counted 0 to 23 lady beetles per card in 2019, with a mean of 0.63 ± 1.66 over the course of the season, and 0 to 42 lady beetles per card in 2021, with a mean of 1.52 ± 2.71. The most common species were *Harmonia axyridis* Pallas (27%), *Brachiacantha spp.* (18%), *Coleomegilla maculata* DeGeer (16%), *Propylea quatuordecimpunctata* L. (16%) and *Coccinella septempunctata* L. (12%).

Contrary to our hypothesis, we found evidence that lady beetle abundance was influenced by natural habitat area and habitat type but not aphid availability or temporal continuity

(Figure 1.3, Table 1). Across a gradient of low (~10%) to high (~80%) semi-natural habitat cover within a 1.5 km radius landscape, average lady beetle counts increased approximately 300% in 2019 ($p = 0.002$) and 160% in 2021 ($p = 0.020$). In contrast, there was no statistical evidence of a relationship between lady beetle counts and total aphid amount or aphid continuity in either year (Table 1).

Lady beetle abundance also varied by habitat type (Figure S1.5, Table 1). In 2019 (a lower-beetle year), there was strong evidence counts were similar across crop habitats but about 50% lower in grassland ($p = 0.003$) and over 80% lower in woodlands ($p<0.001$) compared to corn fields. In 2020 (a higher-beetle year), there was weak evidence that counts compared to corn were 35% higher in soybean ($p = 0.072$), and strong evidence they were about twice as high in alfalfa fields ($p<0.001$) and grasslands ($p = 0.004$) but 50% lower in woodlands ($p = 0.005$).

Sentinel prey experiment

We found moderate evidence that that predation of sentinel egg cards varied by the amount of semi-natural habitat in the landscape ($p = 0.044$) and local habitat type, but not landscape-scale aphid amount or continuity (Figure 1.4, Table 1.2). Average egg predation increased approximately 50% as semi-natural habitat increased from 10% to 80% in the landscape; for corn, soy, alfalfa, small grains, this relationship was not statistically different from the overall mean. However, there was evidence of an interaction for grassland patches, where the benefit of increasing semi-natural habitat in the landscape was about two-times greater (*p* = 0.022) and for woodland patches, where egg predation decreased across the landscape gradient (*p*<0.001).

Discussion

Spatio-temporal resource tracking by mobile consumers is an appealing theoretical framework to explain why agricultural landscape complexity may in some cases enhance natural enemy populations and biological pest control (Iuliano and Gratton 2020, Abrahms et al. 2021). We sought to test this framework by measuring aphids, lady beetles, and predation services at fine spatial and temporal grain and comparing novel resource-based landscape indices with semi-natural habitat area, a traditional landcover-based proxy for resource availability. Our results show that not all habitat is created equal: temporal patterns of resources availability—in this case aphid prey—varied within the broad categories of "crop" and "natural" patches within agricultural landscapes. We hypothesized that resource availability, rather than land cover per se, would be better predictors of predators and pest control services, due the direct trophic relationship between predators and prey. We found, however, that, neither the total amount of aphids nor their temporal continuity in the landscape predicted adult lady beetle populations or predation. On the other hand, the amount of semi-natural habitat in the landscape was consistently positively correlated with total lady beetle abundance in two study years, and with predation rates of sentinel eggs in a one-year experiment.

Our finding that lady beetle populations are correlated with semi-natural habitat is consistent with similar past studies in the U.S. Midwest (Gardiner et al. 2009a, 2009b, Woltz and Landis 2014) and others regions around the world (Elliott et al. 2002, Yang et al. 2019). The fact that our study used a unique methodological (i.e. sampling entire landscapes of multiple habitat types, rather than single focal fields of the same habitat) and analytical approach suggests that this relationship is robust.

While semi-natural habitat may not consistently predict natural enemy abundance across all species, crop types, and geographies (Karp et al. 2018), our result highlights that predictions for particular systems can be reliable. This insight supports an "archetype" approach (sensu Alexandridis et al. 2022) to studying and designing agroecosystems for conservation biological control. By integrating trait-based ecology with salient landscape and management conditions, researchers and practitioners may be able to avoid the pitfalls of overly general conceptual models for beneficial insect conservation (Tamburini et al. 2020).

The finding that predation increased with surrounding semi-natural habitat area is also consistent with previous studies in the region. Like us, Werling et al. (2011) used sentinel corn earworm egg cards, but compared effects only in corn fields and grasslands. They found that grasslands had higher predation rates than corn fields, and that predation increased with forest cover and herbaceous perennials in the landscape. This is in line with our finding that surrounding semi-natural habitat enhanced predation, especially in grasslands. Interestingly, we found that predation in woodlands exhibited the opposite relationship with semi-natural habitat. This could be due to a dilution effect, whereby woodland predators in low-crop landscapes had ample prey available and thus ignored sentinel eggs. Additionally, our experiment was only conducted in the understory, and thus may not have accurately captured predator activity in woodlands.

This study was designed to examine lady beetle abundance patterns across landscapes that were expected to independently vary in the total abundance and temporal continuity of potential prey. We did in fact observed substantial local heterogeneity in the phenology and total amount of aphids, depending on vegetation type. While this finding is perhaps expected, it is nevertheless an important phenomenon to document and elaborate in order to generate and test specific hypotheses about the effect that resource bottlenecks may have on mobile fauna in heterogeneous landscapes (Schellhorn et al. 2015). The existence of patch-level variation in the timing of resource availability is a necessary condition for resource tracking at the landscape level (Abrahms et al. 2021). That we found evidence of such variation indicates that predator population limitation due to discontinuous prey availability is theoretically possible in our study region.

That we did not find evidence of a relationship between increased temporal continuity of resources and the abundance of lady beetle community raises several ecological and methodological explanations. First, by aggregating all lady beetles together in our analysis, we may have missed species-specific relationships resulting from distinct life histories. Different species have different diet and habitat preferences (Sloggett et al. 2008, Hodek and Evans 2012) and physiological tolerance to starvation (Tanaka and Itô 1982, Yasuda and Ohnuma 1999, Phoofolo et al. 2008). Linking taxon-specific resource requirements to particular lady beetle species may thus yield clearer patterns. Furthermore, our samples were dominated by highly competitive, naturalized non-native species (nearly 60% of beetles) that may be resilient to fluctuations in resource availability, e.g. through switching to non-aphid prey including intraguild predation and cannibalism (Snyder et al. 2000, 2004, Gardiner et al. 2011).

A second and related possible explanation is that aphid abundance may be a poor predictor of actual food resources for lady beetles. Not all aphids are palatable to all lady beetles (Hodek and Evans 2012), and coccinellids have a surprisingly wide diet breadth that includes many insect taxa as well as plants and fungi (Lundgren 2009, Weber and Lundgren 2009; Chapter 2). Such alternative foods are likely important for lady beetles at points in space and/or time when aphids are scarce. In particular, several of the dominant species in our region such as *H. axyridis* and *C. maculata* are known to utilize pollen (Harmon et al. 2000, Lundgren and Wiedenmann 2004, Bertrand et al. 2019) and nectar (Lundgren and Seagraves 2011) as alternative protein and carbohydrate sources in the early spring. Because we were unable to quantify all potential food sources at the landscape scale, it is likely that our prey continuity metric paints an incomplete picture of lady beetle resources.

Third, non-food resources may be more important drivers of lady beetle populations in our study area. In particular, lady beetles need sites for overwintering and refuge from disturbance. Such sites include forest leaf litter, beneath tree bark, in stone piles or grass tufts, human dwellings, and other sheltered areas (Honěk 2012) that may be hard to come by in landscapes dominated by annual crop fields. On the other hand, lady beetles may be able to forage sufficient prey even in simple landscapes, where they can also take advantage of large resource pulses that come at particular times (e.g. late spring in small grain crops and late summer in corn and soybean). Thus, overwintering sites could be more limiting to lady beetles in these landscapes, which is better captured by a gradient of semi-natural habitat than prey amount or continuity.

Finally, our metric of prey temporal patterns as the within-season variability of prey abundance over time may be inappropriate for quantifying resource (dis)continuity that actually matters for lady beetle development and survival. Similar approaches have been employed in other studies of resource fluctuations in heterogeneous landscapes (e.g. Hemberger et al., in prep; Spiesman et al. 2020) perhaps because the simple metric of variation over time is intuitive, generalizable, and analytically tractable. Yet alternative metrics—such as the number of times a resource falls below a biologically-determined threshold, or the level of resource scarcity at critical developmental stages—might be more appropriate.

Given these idiosyncrasies, it may be the case that accurately measuring resource patterns is too difficult to make the resource tracking approach a tractable method for conservation biological control. Indeed, landcover may be a more wholistic measure of the various ecological factors that matter for certain natural enemy functional groups (Martin et al. 2019, Alexandridis et al. 2022). Nevertheless, the science of landscape-scale resource tracking is relatively young and largely focused on vertebrate animal movement, with standardized approaches and best practices still in development (Iuliano and Gratton 2020, Abrahms et al. 2021). Future research on beneficial insect conservation and ecosystem services should continue to engage with this nascent ecological subfield to enhance both theory and application.

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Tables

Table 1.1 Generalized linear mixed model results for total lady beetle counts for 2019 and 2021, analyzed separately. Fixed effects (top) include the amount of semi-natural habitat (percent of 1.5 km landscape surrounding sampled habitats), season-long landscape-scale aphid totals and continuity, and habitat type in which lady beetles were collected. Landscape variables are standardized to z-scores to enable comparison of effect sizes. Columns show back-transformed response ratios, 95% confidence intervals, and *p*-values. Random effects (bottom) include sampling patch and landscape to account for non-independence.

	Lady beetle counts 2019			**Lady beetle counts 2021**		
Predictors	*Ratio*	*CI*	*p*	*Ratio*	*CI*	*p*
Intercept	0.72	0.51 – 10	**0.049**	1.07	0.83 – 1.38	0.622
Semi-natural habitat	1.46	1.14 – 1.88	**0.002**	1.24	1.03 – 1.49	**0.020**
Aphid total	1.00	0.79 – 1.26	0.990	0.96	0.80 – 1.14	0.641
Aphid continuity	–	–	–	1.07	1.89 – 1.27	0.475
Habitat (soy)	0.82	0.46 – 1.46	0.505	1.35	0.97 – 1.87	**0.072**
Habitat (alfalfa)	0.87	0.42 – 1.79	0.699	2.08	1.38 – 3.12	**<0.001**
Habitat (small grains)	2.01	0.75 – 5.39	0.162	1.94	1.24 – 3.02	**0.004**
Habitat (grass)	0.49	0.30 – 0.78	**0.003**	0.85	0.61 – 1.20	0.356
Habitat (wood)	0.16	0.09 – 0.27	**<0.001**	0.56	0.38 – 0.84	**0.005**
Random Effects						
σ^2	2.08			1.04		
τ_{00}	0.76_{patch}			0.40_{patch}		
	$0.04_{\text{landscape}}$			$0.08_{\text{landscape}}$		
ICC	0.02			0.07		
N	$17_{\text{landscape}}$			$17_{\text{landscape}}$		
	166_{patch}			170_{patch}		
Observations	166			170		
Marginal R^2 / Conditional R^2	0.176 / 0.189			0.112 / 0.173		

Table 1.2 Generalized linear mixed model results with weighted effects coding for sentinel egg predation in 2021. Fixed effects (top) include the effect of semi-natural habitat in the surrounding landscape, landscape-scale aphid totals and continuity, and their interactions with habitat type. Landscape variables are standardized to z scores to enable comparison of effect sizes. Columns back-transformed response ratios, 95% confidence intervals, and *p*-values. Random effects (bottom) include sampling patch and landscape to account for non-independence, and an observation-level random effect to control for overdispersion.

	Proportion eggs predated		
Predictors	*Ratio*	*CI*	*p*
Intercept	1.27	0.60 – 2.69	0.525
Semi-natural habitat	2.31	1.02 – 5.21	**0.044**
Aphid total	0.78	0.35 – 1.71	0.529
Aphid continuity	0.80	0.36 – 1.76	0.573
Habitat (corn)	0.34	0.19 – 0.61	**<0.001**
Habitat (soy)	1.69	0.84 – 3.38	0.140
Habitat (alfalfa)	0.44	0.14 – 1.32	0.143
Habitat (small grains)	1.58	0.47 – 5.34	0.457
Habitat (grass)	2.23	1.17 – 4.23	**0.015**
Habitat (wood)	1.27	0.54 – 2.99	0.580
Semi-natural × corn	1.32	0.51 – 3.37	0.567
Semi-natural × soy	0.83	0.33 – 2.07	0.690
Semi-natural × alfalfa	1.51	0.41 – 5.63	0.536
Semi-natural × small grains	1.03	0.27 – 3.93	0.962
Semi-natural × grass	2.17	1.12 – 4.22	**0.022**
Semi-natural × wood	0.05	0.01 – 0.24	**<0.001**
Aphid total × corn	1.28	0.83 – 1.97	0.262
Aphid total × soy	0.58	0.28 – 1.20	0.142
Aphid total × alfalfa	2.59	0.87 – 7.69	0.087
Aphid total × small grains	1.21	0.19 – 7.70	0.837
Aphid total × grass	0.26	0.08 – 0.82	**0.022**
Aphid total × wood	1.42	0.22 – 9.02	0.710
Aphid continuity × corn	0.90	0.49 – 1.64	0.722
Aphid continuity × soy	0.78	0.23 – 2.64	0.690
Aphid continuity × alfalfa	1.10	0.18 – 6.62	0.919
Aphid continuity × small grains	0.84	0.41 – 1.72	0.637
Aphid continuity × grass	1.16	0.37 – 3.57	0.802
Aphid continuity × wood	1.30	0.66 – 2.58	0.453
Random Effects			
σ^2	7.58		
$\tau_{00\ \mathrm{card}}$	4.29		
$\tau_{00\ \mathrm{patch}}$	1.56		
$\tau_{00\ \mathrm{landscape}}$	2.04		
ICC	0.32		
N_{card}	326		
N_{patch}	166		
$N_{\mathrm{landscape}}$	17		
Observations	326		
Marginal R^2 / Conditional R^2	0.187 / 0.449		

Figures

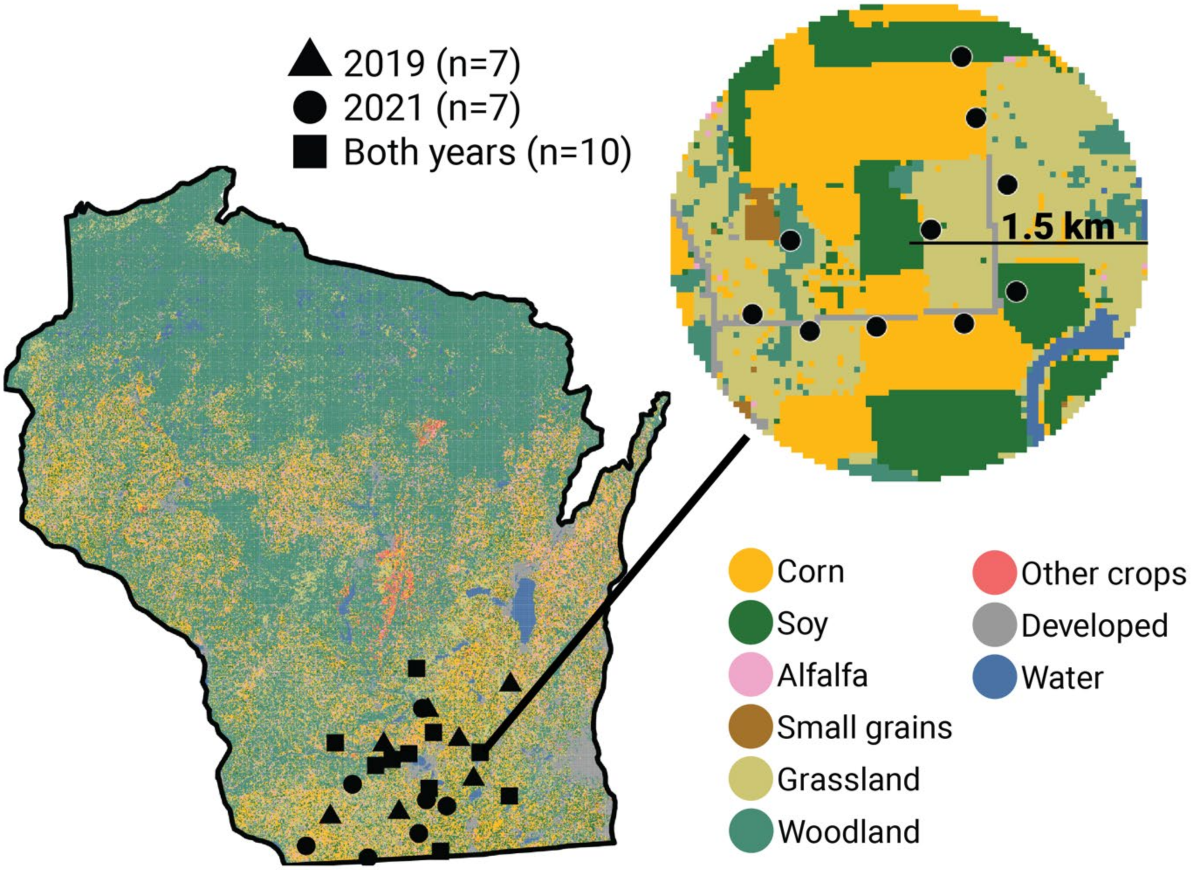

Figure 1.1 Map of sampling landscapes during two years of the study, with expanded sample landscape showing sampling patches distributed across habitat types corresponding to the proportion of landscape area they occupy. Field surveys occurred in patches of habitats in the lefthand column.

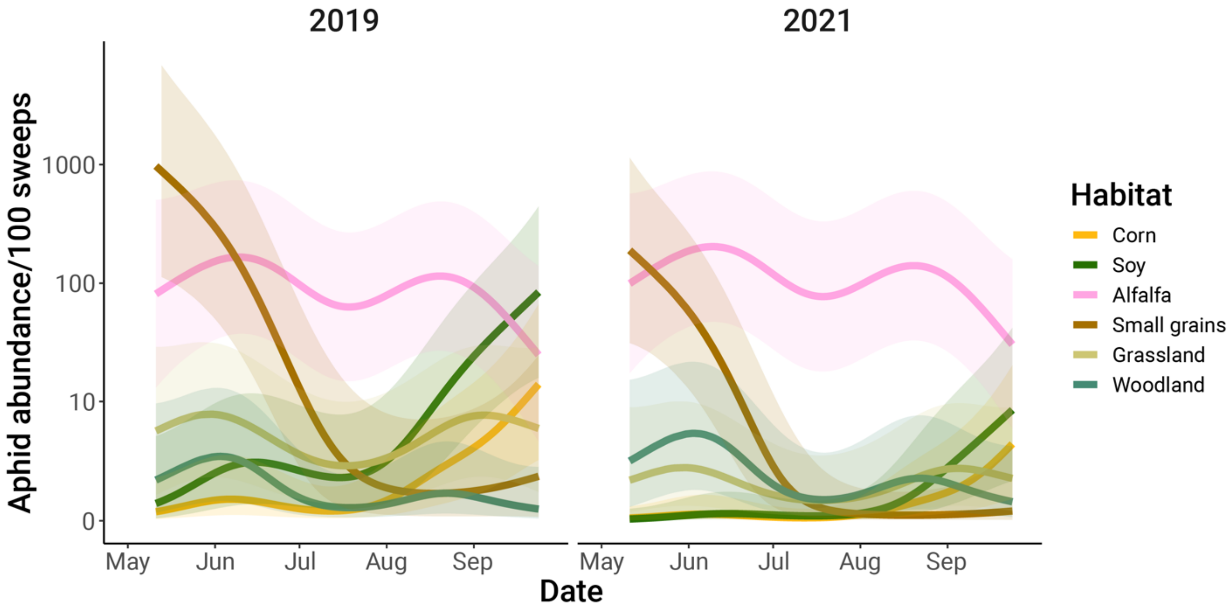

Figure 1.2 Generalized additive mixed model results for aphid counts over time by habitat type and year. Colors represent different habitat and shaded areas depict 95% confidence intervals. Note the logarithmic scale of the y axis.

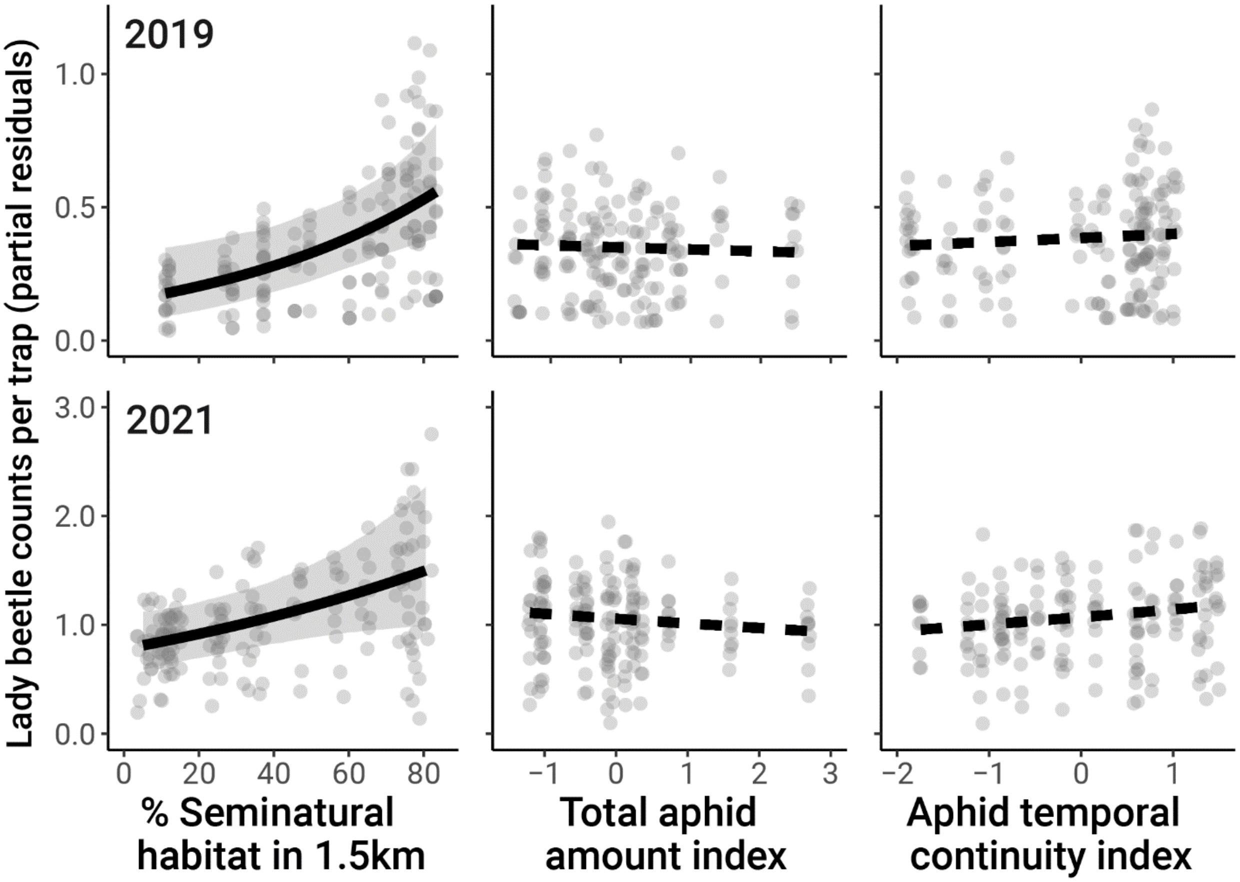

Figure 1.3 Generalized linear mixed model results for the effect of landscape predictors on lady beetle counts on sticky cards. Points are partial residuals at a sampling patch, with all other predictors held at their means, conditioned on the season-long average number of lady beetles per sticky card at a given patch. Solid lines with bootstrapped 95% confidence intervals represent relationships where $p < 0.05$; dotted lines indicate $p > 0.05$. Notice the scale of the y axis differs between years.

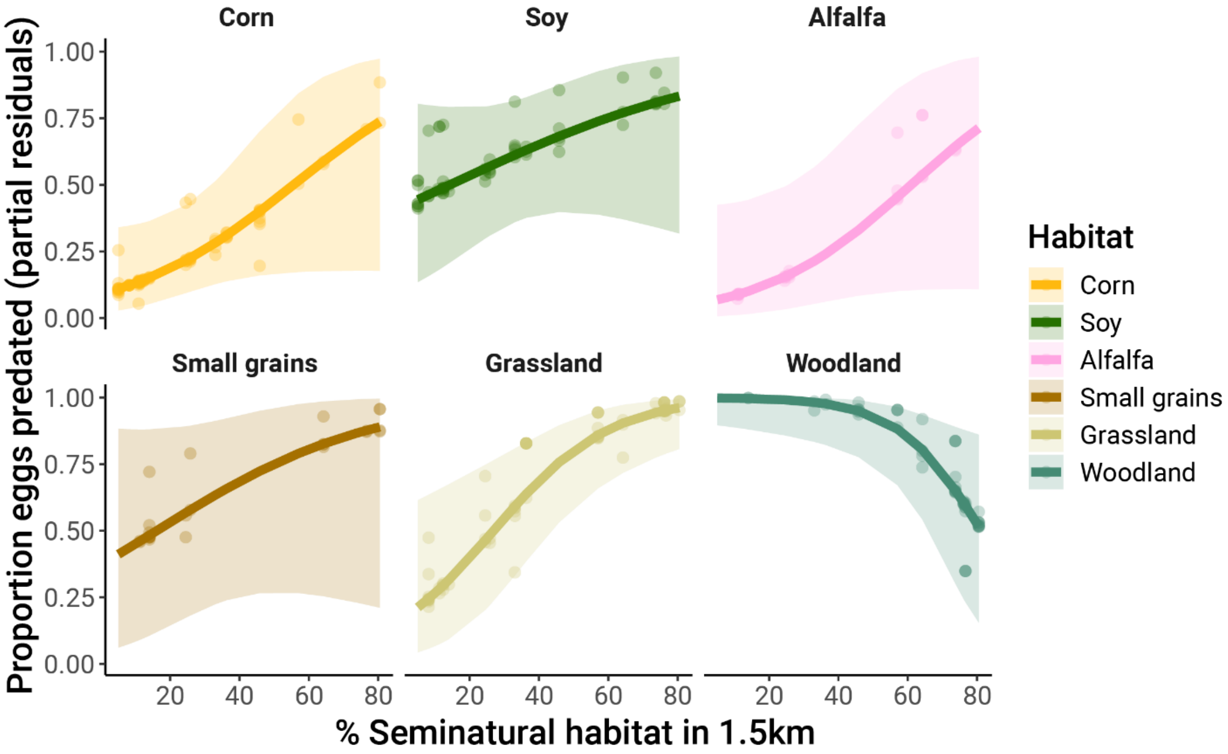

Figure 1.4 Generalized linear mixed model results for the effect of landscape predictors on predation by habitat. Points are partial residuals of the proportion of eggs predated on one egg card after approximately 24 hours in the field, with all other predictors held at their means.

Supplementary material

Table S1.1 Aphid count contrasts for habitat and year in a generalized additive mixed effects model. The first set of contrasts compare years by habitat type; the second set of contrasts compare habitat types to each other within each year. Columns show mean ratios (log response ratio of the mean estimate of the first level to the second level, back-transformed to the response scale) standard error, degrees of freedom, lower and upper confidence intervals, t-statistics, and Bonferroni corrected *p*-values.

Habitat	*Year*	*Contrast*	*Ratio*	*SE*	*df*	*lower*	*upper*	*t*	*p*
Corn		2021 / 2019	0.300	0.092	1808	0.113	0.799	-3.937	0.003
Soy		2021 / 2019	0.101	0.039	1808	0.029	0.344	-5.982	<0.001
Alfalfa		2021 / 2019	1.224	0.538	1808	0.300	5.003	0.460	1.000
Small grains		2021 / 2019	0.195	0.126	1808	0.025	1.537	-2.536	0.407
Grass		2021 / 2019	0.315	0.094	1808	0.121	0.818	-3.876	0.004
Wood		2021 / 2019	1.645	0.538	1808	0.578	4.684	1.524	1.000
	2019	Soy / Corn	4.476	1.772	1808	1.260	15.897	3.786	0.006
		Alfalfa / Corn	146.406	65.439	1808	34.996	612.494	11.156	<0.001
		Alfalfa / Soy	32.712	16.164	1808	6.723	159.165	7.058	<0.001
		Small grains / Corn	5.356	3.288	1808	0.750	38.230	2.734	0.227
		Small grains / Soy	1.197	0.769	1808	0.153	9.359	0.280	1.000
		Small grains / Alfalfa	0.037	0.025	1808	0.004	0.313	-4.933	<0.001
		Grass / Corn	5.955	1.946	1808	2.092	16.954	5.461	<0.001
		Grass / Soy	1.331	0.521	1808	0.380	4.661	0.730	1.000
		Grass / Alfalfa	0.041	0.018	1808	0.010	0.164	-7.346	<0.001
		Grass / Small grains	1.112	0.681	1808	0.156	7.909	0.173	1.000
		Wood / Corn	1.185	0.406	1808	0.396	3.551	0.497	1.000
		Wood / Soy	0.265	0.108	1808	0.072	0.973	-3.270	0.039
		Wood / Alfalfa	0.008	0.004	1808	0.002	0.034	-10.681	<0.001
		Wood / Small grains	0.221	0.137	1808	0.030	1.610	-2.433	0.542
		Wood / Grass	0.199	0.064	1808	0.071	0.557	-5.020	<0.001
	2021	Soy / Corn	1.500	0.601	1808	0.416	5.416	1.012	1.000
		Alfalfa / Corn	597.236	247.559	1808	158.395	2251.907	15.421	<0.001
		Alfalfa / Soy	398.103	177.536	1808	95.469	1660.083	13.424	<0.001
		Small grains / Corn	3.481	1.794	1808	0.668	18.129	2.420	0.562
		Small grains / Soy	2.320	1.255	1808	0.411	13.110	1.556	1.000
		Small grains / Alfalfa	0.006	0.003	1808	0.001	0.033	-9.472	<0.001
		Grass / Corn	6.249	2.264	1808	1.959	19.936	5.057	<0.001
		Grass / Soy	4.165	1.648	1808	1.174	14.783	3.606	0.011
		Grass / Alfalfa	0.010	0.004	1808	0.003	0.039	-11.168	<0.001
		Grass / Small grains	1.795	0.917	1808	0.350	9.214	1.145	1.000
		Wood / Corn	6.500	2.529	1808	1.870	22.591	4.811	<0.001
		Wood / Soy	4.333	1.811	1808	1.136	16.522	3.508	0.017
		Wood / Alfalfa	0.011	0.005	1808	0.003	0.043	-10.472	<0.001
		Wood / Small grains	1.868	0.981	1808	0.347	10.040	1.189	1.000
		Wood / Grass	1.040	0.384	1808	0.319	3.389	0.107	1.000

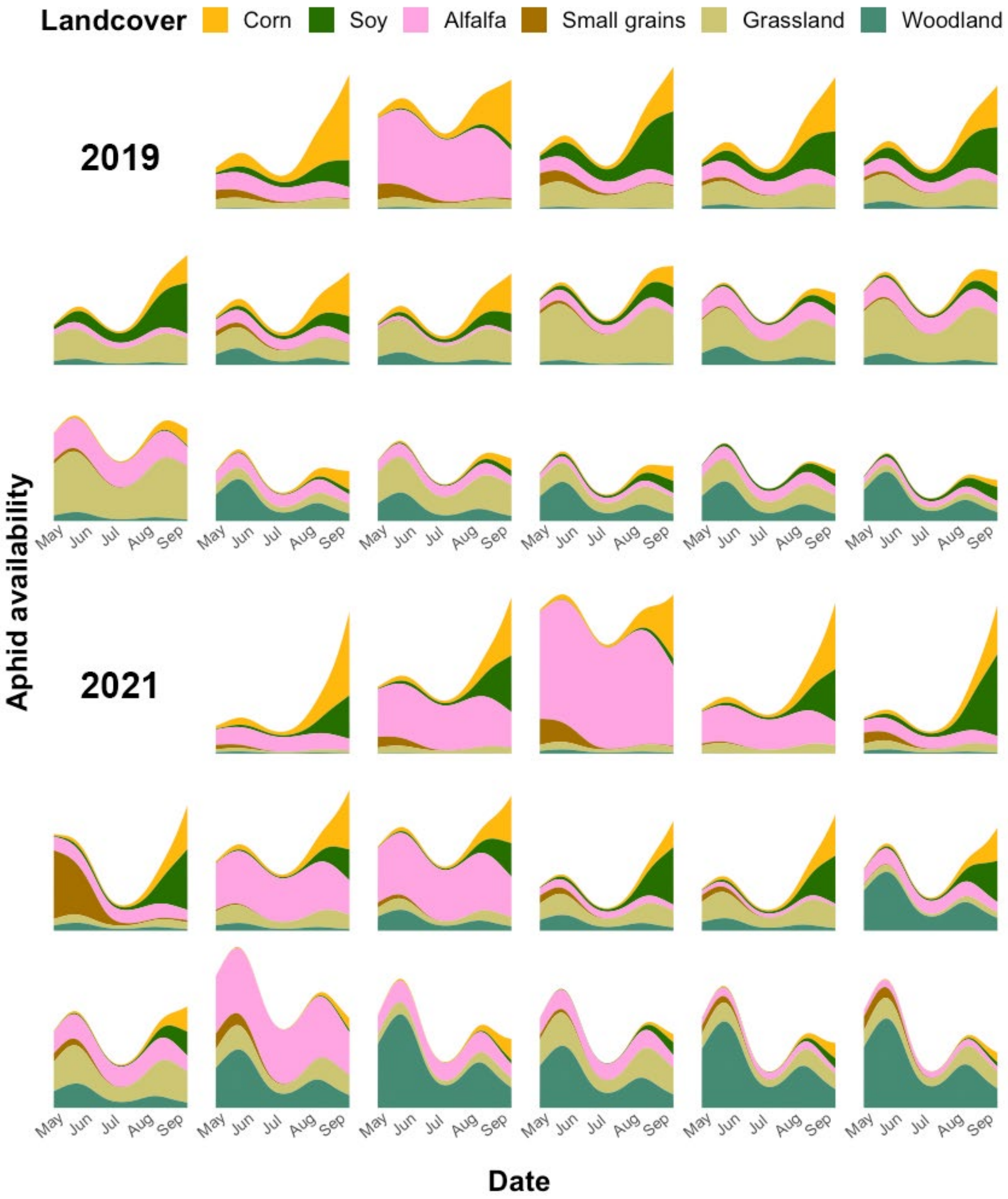

Figure S1.1 Illustration of aphid phenology curves for all landscapes in 2019 and 2021. Colors represent the relative contributions from different habitat types (colors). Panels are arranged in order of semi-natural habitat in a 1.5 km radius.

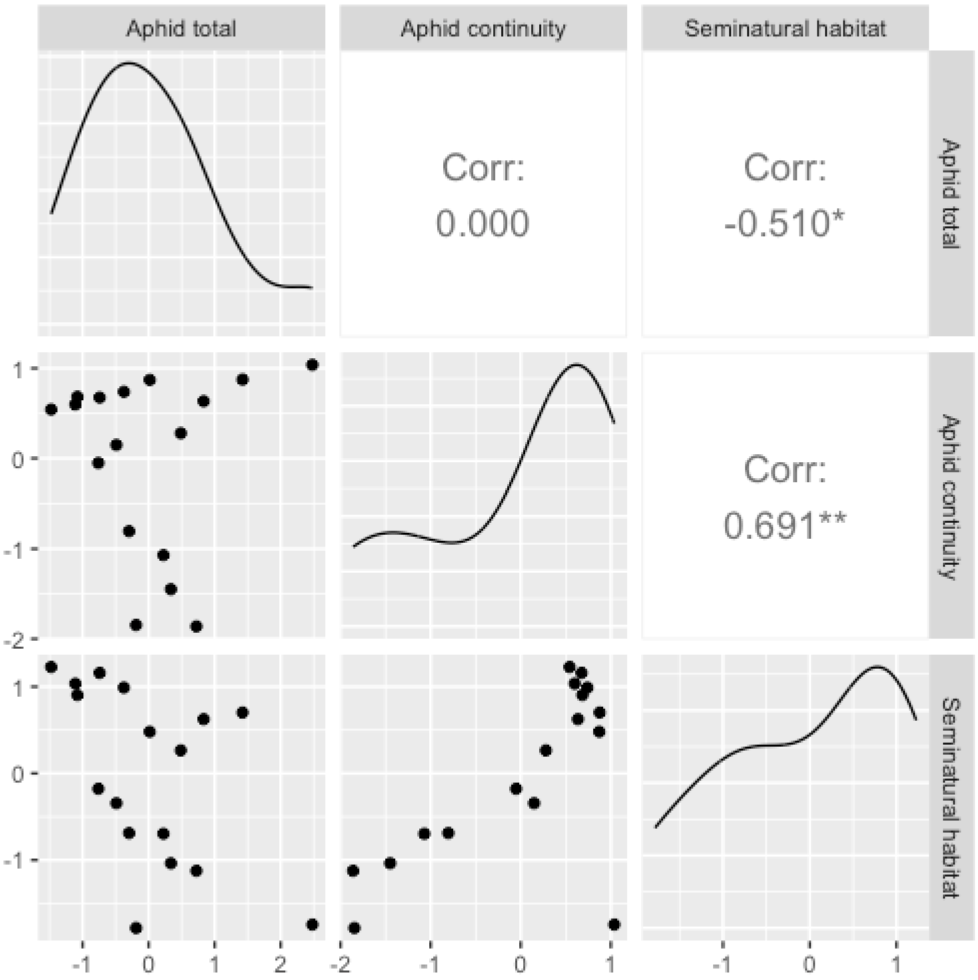

Figure S1.2 Correlation plot for landscape predictors used in models of lady beetle abundance for 2019

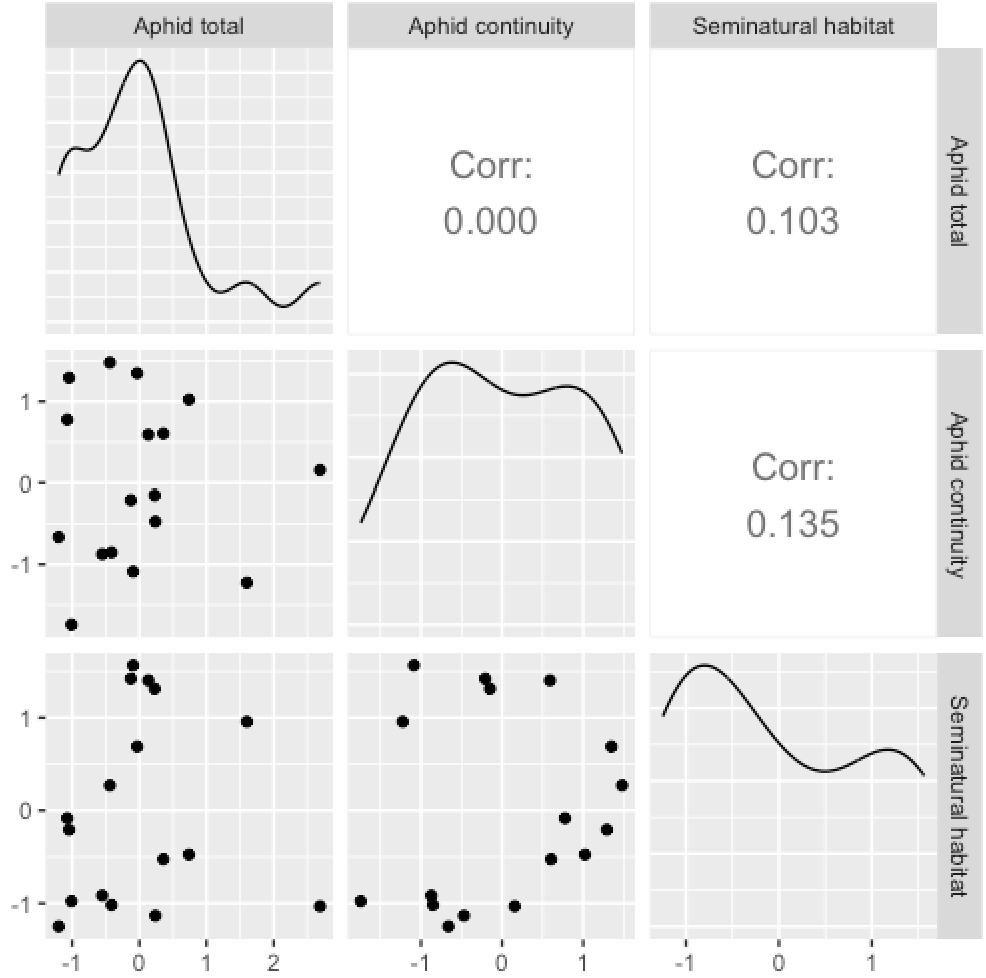

Figure S1.3 Correlation plot for landscape predictors used in models of lady beetle abundance for 2021

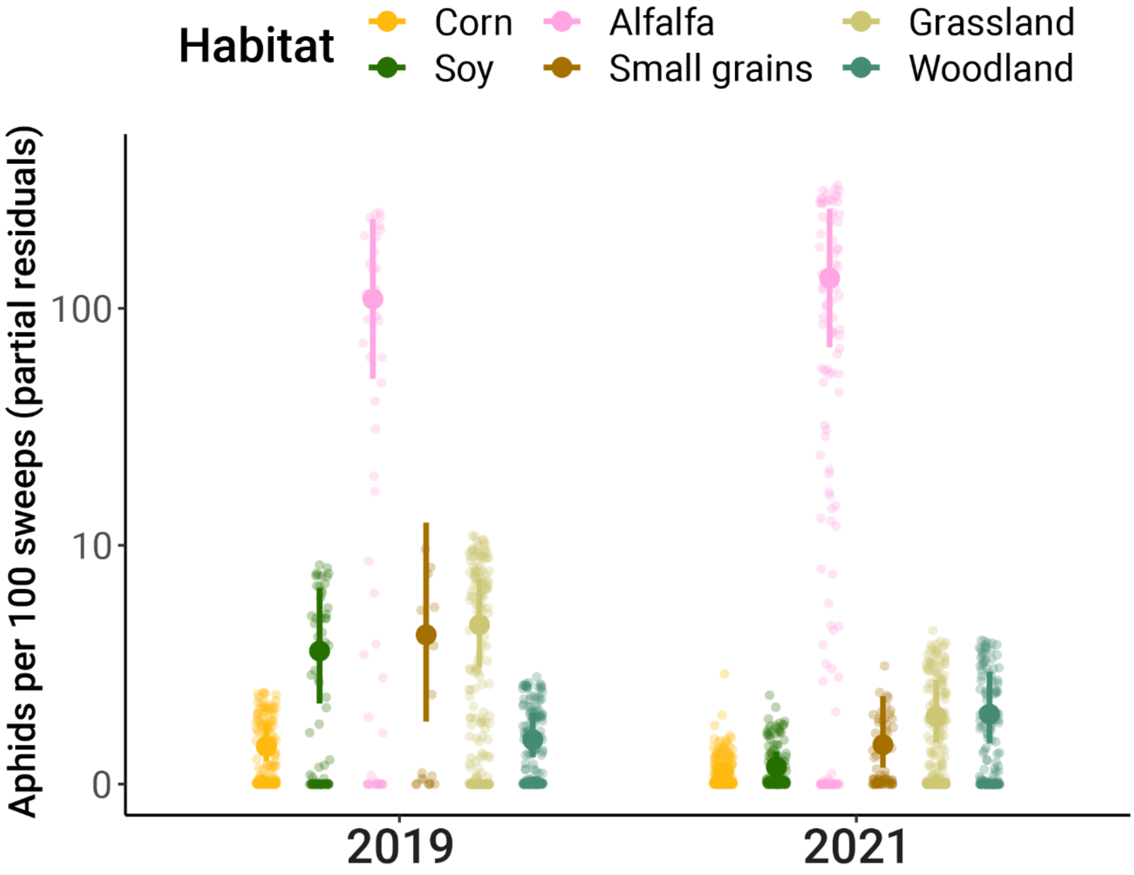

Figure S1.4 Model results for aphid counts by habitat and year. Colors represent different habitats. Small transparent points are partial residuals, with all other predictors held at their means. Large solid points are means, and error bars depict 95% confidence intervals. Note the logarithmic scale of the y axis.

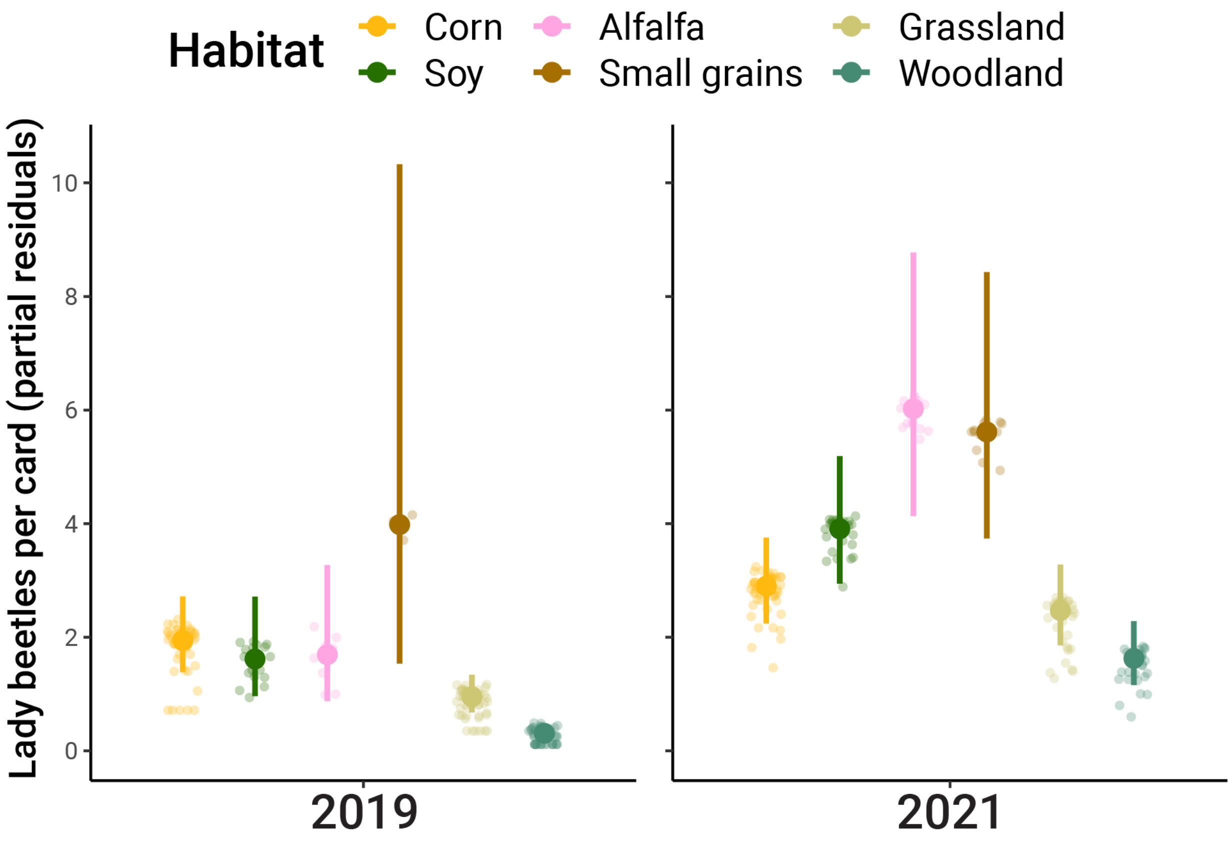

Figure S1.5 Model results for lady beetle counts by habitat in two study years (modeled separately). Colors represent different habitats. Small transparent points are partial residuals, with all other predictors held at their means. Large solid points are means, and error bars depict 95% confidence intervals.

Chapter 2

Complex landscapes, complex diets: DNA metabarcoding reveals lady beetle prey richness increases with landcover diversity

Abstract

Understanding the capacity of mobile organisms to take advantage of resources across different patches in a landscape can reveal strategies for their conservation. For example, high levels of non-crop habitat and landcover diversity in agricultural areas is expected to benefit generalist predators who can fortify their diets with prey resources from multiple adjacent habitats. For some taxa such as lady beetles (Coccinellidae), dietary diversity is associated with improved fitness, but foraging patterns in real landscapes are hard to measure. Here we employed a DNA metabarcoding approach to explore how the presence and taxonomic richness of arthropod prey in lady beetle diets varied by local habitat (crop vs. non-crop) and landscape complexity (non-crop habitat and landcover diversity in a 250 m radius). We collected over 500 individual lady beetles from mixed landscapes in 2019 and 2021, performed whole-body DNA extractions, amplified arthropod DNA using primers optimized for insectivore diets, and used Illumina sequencing to characterize the taxonomic diversity of prey. We found 50 unique prey taxa in lady beetle guts from eight arthropod orders (mostly flies, true bugs, and thrips). Lady beetles in high-crop landscapes were slightly more likely to have prey in their gut, and community-level prey richness was strongly positively correlated with surrounding landcover diversity. This effect was dampened slightly in high-crop landscapes, likely due to smaller prey species pools. Our results enhance knowledge of lady beetle trophic ecology and demonstrate that landscape supplementation may be an important mechanism for the success mobile generalists in complex landscapes.

Author contributions Ben Iuliano, Claudio Gratton, Tania Kim, and Brian Spiesman conceived of and designed the study. Ben Iuliano led field work, sample processing, data analysis, and wrote the first manuscript draft. Claudio Gratton reviewed and contributed to subsequent drafts.

Introduction

Increasing the complexity of farmed landscapes has the potential to conserve biodiversity and enhance ecosystem services (Tscharntke et al. 2005, Sirami et al. 2019, Haan et al. 2021). Landscape supplementation and complementation are two proposed mechanisms by which complex landscapes may be favorable to mobile fauna that can track spatially variable resources (Dunning et al. 1992). Landscape supplementation is the process in which an organism benefits from accessing substitutable resources (e.g. different types of food) in adjacent habitat patches in a mixed landscape. For example, wild bees may forage for nectar and pollen in meadows as well as adjacent flowering crop fields (Mandelik et al. 2012, Mallinger et al. 2016, Martins et al. 2018). Landscape complementation occurs when an organism accesses non-substitutable resources (e.g. food and shelter) in distinct habitat types in a landscape (Ouin et al. 2004, Haynes et al. 2007, Clake et al. 2022).

Landscape elements that have high potential to contribute to resource complementation and supplementation include non-crop habitat and a diversity of landcover types. In landscapes with less cropland and more habitat diversity, mobile organisms are hypothesized to be more likely to have access multiple limiting resources in close proximity to each other, contributing to enhanced health, survival, reproduction, and population stability (Dunning et al. 1992). If the organisms benefiting from these processes also provide ecosystem services (e.g. pollination, predation of crop pests) landscape complexity can also enhance crop production and decrease reliance on inputs (e.g. managed honey bees, chemical pesticides).

The realization of such benefits in agricultural landscapes depends upon the life histories of the particular organisms involved and dimension of landscape complexity under consideration (Haan et al. 2021, 2021). For example, species that have wider diet breadths may be more likely to benefit from retention of uncropped areas and/or increasing crop diversity, since they can take advantage of trophic resources in multiple crop and non-crop habitat types (Iuliano and Gratton 2020). Evaluating the extent to which particular species actually use resources from distinct habitats, and if so which ones, could provide valuable knowledge for more effective agroecological landscape design.

Lady beetles (family Coccinellidae) are common insect predators in agricultural systems that often contribute to natural pest control (Obrycki and Kring 1998, Costamagna and Landis 2006, Obrycki et al. 2009, but see Kindlmann et al. 2015). While often thought of as specialists on small, soft bodied insects (e.g. aphid or scales), lady beetles are known to opportunistically consume a variety of alternative prey (Weber and Lundgren 2009, Evans 2009). Lady beetles can be reliable predators of target prey in controlled environments, but realized foraging in real landscapes are harder to predict and measure. Controlled laboratory experiments have demonstrated that dietary diversity can mitigate negative effects of low-quality prey on lady beetles, in some cases shortening development time, improving growth and/or increased fecundity (Evans et al. 1999, Harwood and Obrycki 2005, Stowe et al. 2021). Thus, landscapes that provide lady beetles with a diverse buffet of prey resources should also enhance their populations and predation services. Simple landscapes have been shown to have negative effects on lady beetle body condition (Tiede et al. 2022) and alter their gut microbiome, likely mediated by prey availability and diversity (Tiede et al. 2017). Yet, to our knowledge no study has yet linked landscape conditions to lady beetle diet composition.

Real-world arthropod diets and predator-prey interaction networks are notoriously difficult to characterize. Traditional methods including direct observation (Warreen and Tadic 1967, Groden et al. 1990), gut dissection and microscopy (Triltsch 1997, 1999) and frass analysis (Davidson and Evans 2010), and stable isotope analysis (Forbes and Gratton 2011) are time consuming, prone to inaccuracies, and biased against soft-bodied prey items and early insect life stages (eggs and larvae) that may comprise large portions of arthropod predator diets. Advances in next-generation sequencing (NGS) technologies have contributed to an explosion of ecological studies that use DNA metabarcoding (Alberdi et al. 2019) to characterize animal diets and evaluate biological control services provided by predatory arthropods (Furlong 2015, González-Chang et al. 2016, Lue et al. 2022).

Two published studies have employed laboratory- and field-based techniques to refine methods for evaluating lady beetle diets using DNA metabarcoding. Amman et al. (2020) developed a novel aphid-specific primer, and found that aphid detection and composition differed between lady beetle collection method and species. Kim et al. (2022) assessed the entire prey community of field-collected lady beetles and found that the diet breadth of beetles collected from a grassland and soybean field was higher than the diet breadth of beetles collected from a corn field, but observed no difference in prey richness per beetle among habitat types. Neither study was spatially replicated, limiting their ability to make inferences about how lady beetle diets may vary with local habitat or landscape context.

In this study, we used NGS of lady beetles collected from agricultural landscapes in southern Wisconsin to explore sources of variation in the composition and richness of their diets. Specifically, we investigated how lady beetle diets varied by lady beetle species and local and landscape habitat context. In two growing seasons, we collected lady beetles of eight species from six habitat types in landscapes selected to span gradients of proportion cropland and land cover diversity in the surrounding area. We predicted that prey detection rates and dietary richness would be higher in non-crop (grassland and woodland) sites, negatively correlated with the proportion of cropland in the landscape, and positively correlated with landscape diversity.

Methods

Field sampling

We collected adult lady beetles in two years (2019 and 2020) from agricultural fields and natural habitat areas in Southern Wisconsin, USA. There are at least 15 native species of lady beetles (Coccinellidae) in the region (Gardiner et al. 2009b, 2021, Chapter 1), but a large portion of the community comprises introduced species. We restricted our collection to the most commonly encountered species: the native *Coleomegilla maculata*, *Cycloneda munda*, *Hippodamia convergens*, and *Hippodamia parenthesis*; and the introduced *Harmonia axyridis*, *Coccinella septempunctata*, *Propylea quatuordecimpunctata*, and *Hippodamia variegata*. While each of these species has unique life history traits, they all display some level of polyphagy (i.e. consume prey from multiple families) and were encountered in several habitat types during field surveys (Chapter 1). We collected only adult beetles, which we assumed would be able forage across multiple habitat patches in the landscape (unlike the less-mobile larvae).

We focused our sampling in six dominant land covers classes found in our study region, grouped into crop and non-crop habitats. Crops included corn; soybean; alfalfa; wheat, oats, and rye ("small grains"). Non-crop habitats included perennial pastures, herbaceous wetlands, prairies ("grasslands"); woodlots and forests ("woodlands"). Collection sites were designated in 17 landscapes in each of the two study years (see Chapter 1 for a more detailed description of survey design). Adult lady beetles were sampled opportunistically using sweep nets and aspirators (BioQuip, Rancho Dominguez, CA) across 5-7 site visits between May and September. We attempted to collect at least 2 and up to 10 beetles per species per sampling event. Upon collection, lady beetles were transferred to individual microcentrifuge tubes and placed on ice. Samples were brought back to the lab and stored at -20°C until further processing.

Sample processing and DNA sequencing

We extracted DNA from 509 whole lady beetles using the DNeasy Blood & Tissue Kits (Qiagen, Valencia CA, USA). Extracted DNA was amplified using primers specific to the mitochondrial cytochrome c-oxidase subunit I region (COI) designed for analysis of insectivorous animal diets (Jusino et al. 2019). The sequences of these primers that were complementary to the COI locus were LCO1490: 5′- GGTCAACAAATCATAAAGATAT TGG-3′ and CO1-CFMRa: 5′-GGWACTAATCAATTTCCAAATCC-3′. Amplification conditions were as follows: 95°C for 15 min, 35 cycles of 94°C for 30 s, 51°C for 30 s and 72°C for 90 s, and a final extension of 72°C for 10 min. Random samples of PCR products were visualized via gel electrophoresis to confirm amplification. All samples were then plated, with 2-6 negative controls (blanks) included on each 96-well plate.

PCR products were submitted to the University of Wisconsin Biotechnology Center for library preparation and sequencing. Samples were sequenced in four pooled runs using Illumina NovaSeq 6000 with paired-end, 150 base pair sequencing. Targeted read depth was 3 million reads per 96-well plate (approximately 30,000 reads per sample).

The data generated from the Illumina sequencing were processed and analyzed using Quantitative Insights Into Microbial Ecology (QIIME2) version 2 2020.8 (Bolyen et al. 2019). Sequencing reads were denoised and quality filtered using the denoising program Divisive Amplicon Denoising Algorithm (DADA2; Callahan et al. 2016). DADA2 was used to trim low quality bases, filter out noisy sequences, correct errors in marginal sequences, merge overlapping paired end reads and remove chimeric sequences and singletons, and then dereplicate those sequences. The resultant dereplicated sequences are termed as “Amplicon sequence variant (ASV)”. Sequence variants were aligned and masked using MAFFT (Katoh et al. 2002) and the phylogenetic tree of the ASV’s created using FastTree (Price et al. 2009). Low frequency reads and index bleed through between sequence runs estimated to be 0.1% of the reads were removed from the analysis. Finally, taxonomy was assigned using a hybrid method, a combination of VSEARCH (Rognes et al. 2016), UTAX and SINTAX (Edgar 2016) from the Amplicon Toolkit Pipeline (AMPtk; Palmer et al. 2018) to the mitochondrial COI region. The COI database used for the taxonomy classification consists of both arthropod and chordate and is pulled from the BOLDv4 database (Ratasingham and Hebert 2007). All non-arthropod reads were excluded from the analysis.

Following initial sequence processing and quality filtering, Actual read depth per sample ranged from 118 to 629,917 reads, with an average of 271,614, 10,652, 41,759, and 14,944 reads per sample for each of the four sequencing runs. Eight samples had fewer than 500 reads and were removed from the analysis.

After reads were assigned to operation taxonomic units (OTUs) separately for each pool, reads with matching OTUs were aggregated and data from all 4 pools were combined for subsequent quality filtering. We constructed a prey OTU presence/absence matrix following best practices for controlling false positives in metabarcoding data (Deagle et al.

2019, Drake et al. 2022). We filtered reads by removing those less than or equal to the maximum read count in negative controls per OTU per sequencing run, and used a sample-based threshold of 1% of total reads per OTU per sample. Due to high levels of non-host lady beetle reads (particularly *H. axyridis*) in samples and negative controls (likely due to contamination), we excluded all lady beetle reads from our analysis and thus we were not able to evaluate the potential for intraguild predation. We also removed reads of parasitoids (e.g. *Dinocampus coccinellae*) and taxa which are known not to occur in the study region.

Landscape data

Landscape data were derived from the USDA Cropland Data Layer (CDL) available for each year of the study (USDA NASS n.d.). To reduce the influence of spurious classification and functionally synonymous classes on calculated landscape metrics, we reclassified landcover maps to the most common classes in the region (corn, soybean, alfalfa, small grains, other crops, grassland/pasture, woodland). Retaining the original CDL classification scheme did not qualitatively change results (data not shown). We used the landscapemetrics package (Hesselbarth et al. 2019) to calculate the proportion of cropland and landscape diversity in a 250 m buffer around sampling locations using Simpson's diversity index (following Gardiner et al. 2009a, Tiede et al. 2022). The Simpson index is less sensitive to rare classes than habitat richness or Shannon diversity, making it a more conservative estimate of landscape diversity, though using Shannon diversity produced qualitatively similar results (data not shown). We selected 250 m buffers as a reasonable maximum spatial extent across which we might expect foraging lady beetle adults to travel over the detectability half-life of prey DNA in their gut (typically <12 hours; Chen et al. 2000, Greenstone et al. 2014)

Statistical analyses

All data handling and statistical analyses were conducted in R (R Core Team 2023) with RStudio (RStudio Team 2023). Model assumptions were validated using the DHARMa package (Hartig and Lohse 2022). Data were visualized using the packages ggplot2 (Wickham 2016), ggeffects (Lüdecke et al. 2023), and bipartite (Dormann et al. 2022).

Due to low sample abundance and low prey detection rates for lady beetle species other than *C. maculata*, we present descriptive illustrations rather than formal statistical tests of prey diets among species. To evaluate the effects of local habitat type and landscape context on lady beetle diets, we aggregated all beetles of all species collected per site to calculate a community-wide prey detection rate (proportion of beetles with at least one prey item detected) and prey taxa richness for beetles where prey were present (i.e. prey richness > 0), which were used as response variables in generalized linear mixed models constructed using the glmmTMB package (Brooks et al. 2017). We used a model selection approach to evaluate the importance of local landcover (crop vs. non-crop habitat) and landscape context (% cropland and landcover diversity in a 250 m radius) for lady beetle diets. Full models contained all three standardized predictors and their interactions, with location nested within year as a random effect to account for non-independence, and sample size (number of beetles) as weights. We modeled prey presence with a binomial distribution, and prey richness with a Poisson distribution. We used the dredge function in the package MuMIn (Bartoń 2023) to determine which combination of predictors best explained variation in lady beetle diet data using AICc. We report statistics for all models, and use the top model to visualize results.

Results

Lady beetle and prey species

After sample quality filtering, we retained 492 lady beetles from eight species for analysis (Figure 2.1, Table 2.1). Samples were dominated by *C. maculata* (57%), which was also a dominant species in standardized abundance surveys (Chapter 1), followed by *H. axyridis* (16%), *C. septempunctata* (9%), *P. quadrodecimpunctata* (6%), and *H. variegata* (6%); other species combined comprised the final 6% of samples. Average prey detection rate across all species was 17%, with the highest detection in *C. maculata* (21%) and the lowest in *H. variegata* (4%; Figure 2.1).

We detected 50 unique prey OTUs from 8 arthropod orders in our samples (Table 2.1, Figure 2.2). Prey taxa were dominated by flies (35% of detected prey), true bugs (aphids and mirid bugs, 28%), and thrips (15%).

Local habitat and landscape context

Lady beetles were collected in 159 distinct site-year combinations, 59 of which included at least one lady beetle with at least one prey species detected. Most lady beetles came from corn fields (n=52 site-years), followed by grasslands (n=28), alfalfa fields (n=26), soybean fields (n=23), woodlands (n=17) and small grain fields (n=13). The sample size of lady beetles per site-year ranged from 1 to 22 individuals.

The top model for prey detection at the site level (proportion of beetles with prey detected) included only the percent of cropland within 250 meters of the sampling site (Table 2.2, Figure 2.3). Prey detection increased modestly with increasing proportion cropland (β = 0.40, CI: 0.14, 0.71). Models with ΔAICc < 2 also included landscape diversity and its interaction with percent cropland (Table 2.2), but 95% confidence intervals for these terms contained zero, suggesting they were not important predictors of prey detection.

The top model for prey taxa richness included habitat type, proportion cropland within 250 m, and their interaction, as well as landscape diversity and its interaction with proportion cropland (Table 2.3). Increasing proportion cropland in the surrounding landscape was positively correlated with prey richness in lady beetles collected from cropland (β = 0.31, CI: 0.17, 0.45) but negatively correlated with prey richness for beetles collected from natural areas (β = -0.39, CI: -0.68, -0.10; Figure 2.4).

There was a strong positive effect of landscape diversity on prey taxa richness (β = -0.51, CI: -0.30, -0.71; Figure 2.5). This was mediated by proportion cropland: at high levels of cropland in the surrounding area, the positive effect of landscape diversity on prey richness slightly decreased (β = -0.24, CI: -0.43, -0.04; Figure 2.6)

Discussion

The ability of mobile consumers to utilize resources from multiple patch types is a key assumption underlying calls to increase landscape complexity for the promotion of biodiversity-based ecosystem services (Tscharntke et al. 2021). Validating this assumption requires the characterization of real-world diets of service-providing species and their response to habitat conditions and landscape structure. In this study, we sought to investigate how the prey taxa consumed by predatory lady beetles varied by beetle species, local foraging habitat, and landscape complexity. We found that lady beetles collected in more diverse, cropped landscapes were more likely to forage on a more diverse set of prey taxa. To our knowledge, this study is the first to document a correlation between the diversity of prey consumed by predatory insects and the landcover diversity of the surrounding area, a finding consistent with the idea that landscape supplementation can be an important ecological process for populations of service-providing organisms (Dunning et al. 1992). Our results contribute to the body of evidence demonstrating that landscape context is an important driver of trophic interactions for mobile consumers, and suggests a mechanism by which complex landscapes contribute to the conservation of predatory insects and their associated pest control services.

Prey detection and taxa richness were predicted by the interaction of several local and landscape habitat variables. The proportion of the surrounding landscape covered by cropland was the only variable that had a measurable effect on prey detection rates, with beetles in crop-dominated landscapes being slightly more likely to contain prey. This may suggest that lady beetles are more actively foraging in these landscapes, reflecting high densities of preferred prey in crop fields (Yasuda and Ishikawa 1999, Donaldson et al. 2007) or that simpler vegetation architecture in cropped landscapes enable lady beetles to spend more time eating and less time navigating and searching for prey (Pervez and Yadav 2018).

For beetles in which prey were detected, taxa richness was positively correlated with the diversity of surrounding land covers, regardless of local habitat type. This finding provides indirect support for inter-habitat movement of lady beetles, and is consistent with the hypothesis that generalist predators are able to take advantage of the eclectic buffet that complex landscapes have to offer (Iuliano and Gratton 2020). It also may partially explain why lady beetle abundance is often correlated with metrics of landscape complexity, at least for some species (Gardiner et al. 2009a, 2009b, Croy et al. 2023, Chapter 1).

Because a majority of the prey taxa detected in lady beetle guts were not habitat specialists (i.e. they can be found in multiple crop and non-crop land cover types), we were unable to make statistical inferences about allochthonous prey. However, in our data there are several examples of lady beetles collected from one habitat detected to contain prey DNA from another habitat. From soybean fields we collected two *C. septempunctata* individuals that were positive for *Acyrthosiphon pisum* (pea aphid, primarily found in alfalfa fields), and from a corn field one *C. maculata* individual that was positive for *Hypera postica* (alfalfa weevil). In alfalfa, we found one *C. maculata* and one *P. quatuordecimpunctata* that were positive for *Leptopterna dolabrata* (meadow plant bug, a grass specialist). These anecdotes may provide evidence of lady beetle foraging across the landscape. An alternative (if less likely) explanation could be that the lady beetles encountered prey in the "wrong" habitat as the prey were traversing the landscape. More intensive sampling of fewer sites could offer a clearer picture of cross-habitat foraging; however, there are inherent constraints to metabarcoding approaches for detecting spatially complementary resource use (i.e. the half-life of prey in predator guts may be shorter than the timespan within which predators typically move to a new habitat patch).

For lady beetles collected from crop fields, a greater proportion of cropland in the surrounding landscape was positively associated with prey taxa richness, while for lady beetles collected from grasslands and woodlands the opposite was true. This could be due to context-specific habitat use patterns by lady beetles. In landscapes dominated by cropland, uncropped areas may not function as important foraging habitat when prey resources in crop fields are abundant (i.e. most of the sampling period). Instead, lady beetles may be using these semi-natural areas as refuge from disturbance (Honěk 2012). Furthermore, the beetles we collected for this study came from ground cover and understory vegetation, missing lady beetles in the canopy where species composition and behavior might be different (Ulyshen and Hanula 2007, Honěk 2012, Cottrell 2017). In contrast, lady beetles in low-crop landscapes may rely more heavily on semi-natural areas for prey, contributing to increased taxa richness in beetles collected from these habitats.

More cropland in the landscape also tempered the positive effect of landscape diversity on prey taxa richness. This likely reflects an inherent ecological difference between high-diversity, low-crop landscapes and high-diversity, crop-dominated landscapes. Low-crop landscapes in our study were dominated by semi-natural grasslands and woodland patches, which contain more diverse plant and corresponding arthropod communities than crop fields (Robertson et al. 2012, Werling et al. 2014). Accordingly, beetles foraging in these landscapes likely had access to a greater breadth of prey taxa than beetles in similarly diverse, crop-dominated landscapes.

Despite low prey detection rates, DNA metabarcoding revealed a remarkably wide diet breadth of the lady beetles in our study, consistent with other research on the trophic interactions of coccinellids (Evans 2009, Hodek and Evans 2012, Kim et al. 2022). Because our samples were dominated by *C. maculata*, we were unable to make reliable comparisons of lady beetle diets by species. For example, we only detected a single prey taxon in a single lady beetle for *H. variegata* (thrips), *H. convergens*, and *Hippodamia parenthesis* (*A. pisum,* pea aphid). More targeted sampling and sequencing of rarer lady beetle species is required to accurately characterize and contrast their diets. Further refinement of laboratory techniques may also be helpful, given the surprisingly low prey detection rate (5%) for the dominant generalist *H. axyridis*. High lady beetle DNA read counts of this species across samples may indicate that it amplified more readily than DNA from co-occurring taxa, potentially obscuring prey detection in these samples. Moreover, among species differences in digestion rate or frequency of feeding could also influence patterns in favor of species with more frequent feeding or slower gut-passage times of prey (Greenstone et al. 2014, Uiterwaal and DeLong 2020).

For *C. maculata* samples, Diptera was the arthropod order with the most prey hits (43% of hits) and highest number of unique prey OTUs (52% of OTUs). Past research has drawn attention to the under-appreciation of flies in lady beetle diets. Using an antibody-based detection system, Moser et al. (2011) showed that late-instar larvae of three lady beetle species, including *C. maculata*, can prey upon flies, though detection rates in larvae were much lower (generally <5%) than in this study of adult lady beetles. Kim et al. (2022) also found that flies were a common prey for adult lady beetles using DNA metabarcoding, but detection rates were still only 13%. Laboratory studies have demonstrated that fruit fly (*Drosophila melanogaster*) larvae (Schultz et al. 2019) and house fly (*Musca domestica*) eggs (Riddick et al. 2014) can serve as high-quality prey items for commercial rearing of C. maculata throughout their entire lifecycle, suggesting that foraging on flies by natural populations is plausible. Several of the fly taxa detected in our samples (e.g. those in the families Chaoboridae and Chironomidae) are aquatic species that reside in freshwater lakes or streams as eggs and larvae. Because these life stages would be inaccessible to lady beetles, it implies that beetles would consume adults of these taxa on vegetation, perhaps as they nectaring at flowers. Alternatively, detection of these species could be due to sample contamination missed by quality filtering.

Other taxa comprising a large portion of lady beetle diets were hemipterans (aphids and mirid bugs) and thrips, which are well-documented as common lady beetle prey. Sixteen prey taxa (32% of OTUs) detected in lady beetle samples were pests known to cause economic damage, including alfalfa weevils (*Hypera postica*), pea aphid (*Acyrthosiphon pisum*), green peach aphid (*Myzus persicae*), tarnished plant bug (*Lygus lineolaris*) and eastern flower thrips (*Frankliniella tritici*). The wide beetle diet breadths found here suggest that lady beetles both contribute to suppression of pests beyond aphids, and rely on a multitude of non-pest species from both crop fields and semi-natural habitats to maintain their populations.

The findings of this study contribute to knowledge of lady beetle trophic ecology and the mechanisms by which landscape structure influences populations of mobile consumers. It is worth noting that the vast majority of beetles in our study were *Coleomegilla maculata*, a native species that has maintained large populations in the region while other native species have declined due to competition from introduced species (Alyokhin and Sewell 2004, Bahlai et al. 2015a, Gardiner et al. 2021). Our findings support speculation that *C. maculata*'s relative stability in the face of invasion could be due to its ability to exploit a wide variety of prey, thus alleviating competitive pressures. Future metabarcoding studies designed to compare the relative diet breadths of different species could further clarify contrasting population trajectories in response to biological invasions and landscape change.

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Tables

Table 2.1 Lady beetle species included in the study by origin, sample size, prey detection rate, and number of unique OTUs identified

Species	origin	n	detection rate (%)	prey OTUs
Coleomegilla maculata, DeGeer	native	281	21	47
Harmonia axyridis, Pallas	introduced	81	5	7
Coccinella septempunctata, L.	introduced	45	18	5
Propylea quatuordecimpunctata, L.	introduced	29	17	3
Hippodamia variegata, Goeze	introduced	28	4	1
Cycloneda munda, Say	native	13	15	1
Hippodamia convergens, Guérin-Méneville	native	9	11	1
Hippodamia parenthesis, Say	native	6	17	1
	Overall	492	17%	50

Table 2.2 Comparison of all models for prey detection in lady beetle samples. All models included an intercept and random effect for location nested within year. Predictors included local habitat type, percent cropland and landscape diversity within 250 m, and their interactions. Values represent standardized coefficients for continuous variables. Total degrees of freedom and difference in Aikake's Information Criterion corrected for small sample sizes (ΔAICc) from the top model are also shown. 95% confidence intervals are shown for models with ΔAICc < 2.

Habitat *(natural vs. crop)*	**% Cropland**	**Landscape diversity**	**% Cropland x Habitat**	**Landscape diversity x Habitat**	**% Cropland x Landscape diversity**	**% Cropland x Landscape diversity x Habitat**	**df**	**ΔAICc**
	0.40 (0.13, 0.67)						4	0.00
	0.43 (0.14, 0.72)	0.30 (-0.11, 0.72)			-0.30 (-0.68, 0.09)		6	1.40
	0.42 (0.14, 0.69)	0.09 (-0.18, 0.37)					5	1.70
0.18 (-0.39, 0.75)	0.42 (015., 0.70)						5	1.75
0.22	0.45	0.30			-0.31		7	3.02
0.16	0.43	0.09					6	3.55
0.18	0.42		0.00				6	3.91
-0.09	0.38	0.00		0.63			7	3.91
0.02	0.41	0.21		0.39	-0.25		8	4.68
							3	5.03
0.23	0.49	0.33	-0.14		-0.33		8	5.08
0.17	0.45	0.09	-0.05				7	5.72
-0.14	0.43	0.01	-0.20	0.69			8	5.80
0.00	0.46	0.23	-0.19	0.45	-0.25		9	6.62
0.36		-0.07		0.93			6	6.92
		0.05					4	7.01
-0.04							4	7.12
-0.08	0.47	0.29	-0.27	0.44	-0.32	0.53	10	8.17
-0.05		0.06					5	9.12

Table 2.3 Comparison of candidate models for prey richness in lady beetle samples. All models included an intercept and random effect for location nested within year. Predictors included local habitat type, percent cropland and landscape diversity within 250 m, and their interactions. Values represent standardized coefficients. Total degrees of freedom and difference in Aikake's Information Criterion corrected for small sample sizes (ΔAICc) from the top model are also shown. 95% confidence intervals are shown for models with ΔAICc < 2.

Habitat *(natural vs. crop)*	**%Cropland**	**Landscape diversity**	**%Cropland x Habitat**	**Landscape diversity x Habitat**	**%Cropland x Landscape diversity**	**%Cropland x Landscape diversity x Habitat**	**df**	**ΔAICc**
0.19 (-0.39, 0.75)	0.31 (0.17, 0.45)	0.49 (0.30, 0.68)	-0.70 (-0.98, -0.41)		-0.27 (-0.22, 0.58)		8	0.00
0.07 (-0.36, 0.50)	0.28 (0.14, 0.43)	0.41 (0.17, 0.64)	-0.70 (-0.99, 0.41)	0.20 (-0.17,0.56)	-0.22 (-0.42, -0.02)		9	1.67
-0.09	0.21	0.20	-0.64	0.41			8	3.26
0.10	0.28	0.39	-0.67	0.22	-0.19	-0.38	10	3.69
0.14	0.22	0.26	-0.60				7	7.29
0.10	0.10	0.18		0.39			7	19.45
0.02		0.15		0.40			6	19.60
0.37	0.16	0.39			-0.19		7	20.21
0.19	0.14	0.29		0.27	-0.12		8	20.70
0.19	0.15		-0.54				6	20.76
	0.13	0.39			-0.18		6	21.54
		0.22					4	22.85
0.33	0.11	0.24					6	22.89
	0.08	0.25					5	23.48
0.24		0.21					5	23.50
0.32							4	31.48
							3	32.65
0.40	0.05						5	33.17
	0.01						4	34.90

Figures

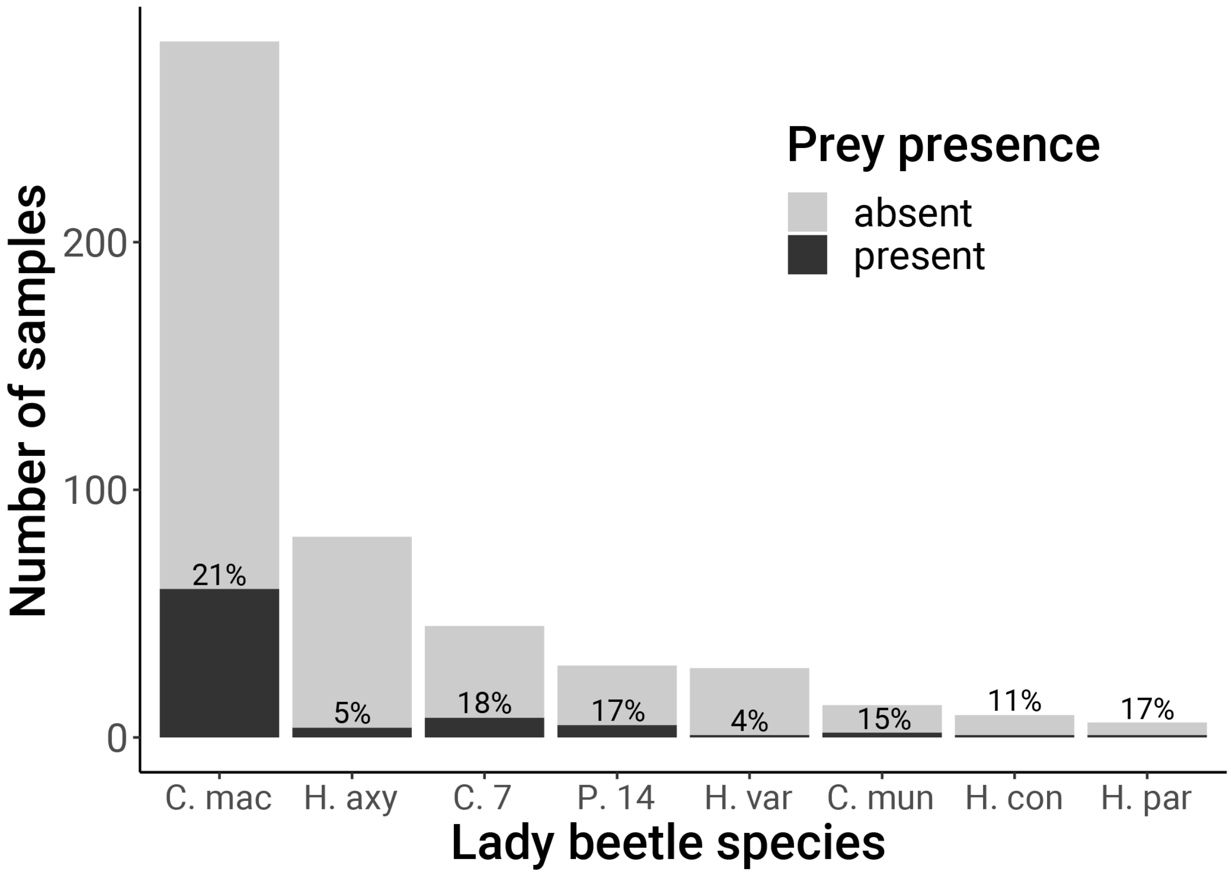

Figure 2.1 Prey detection by lady beetle species. Shaded areas represent beetle samples with at least one prey taxon present after quality filtering.

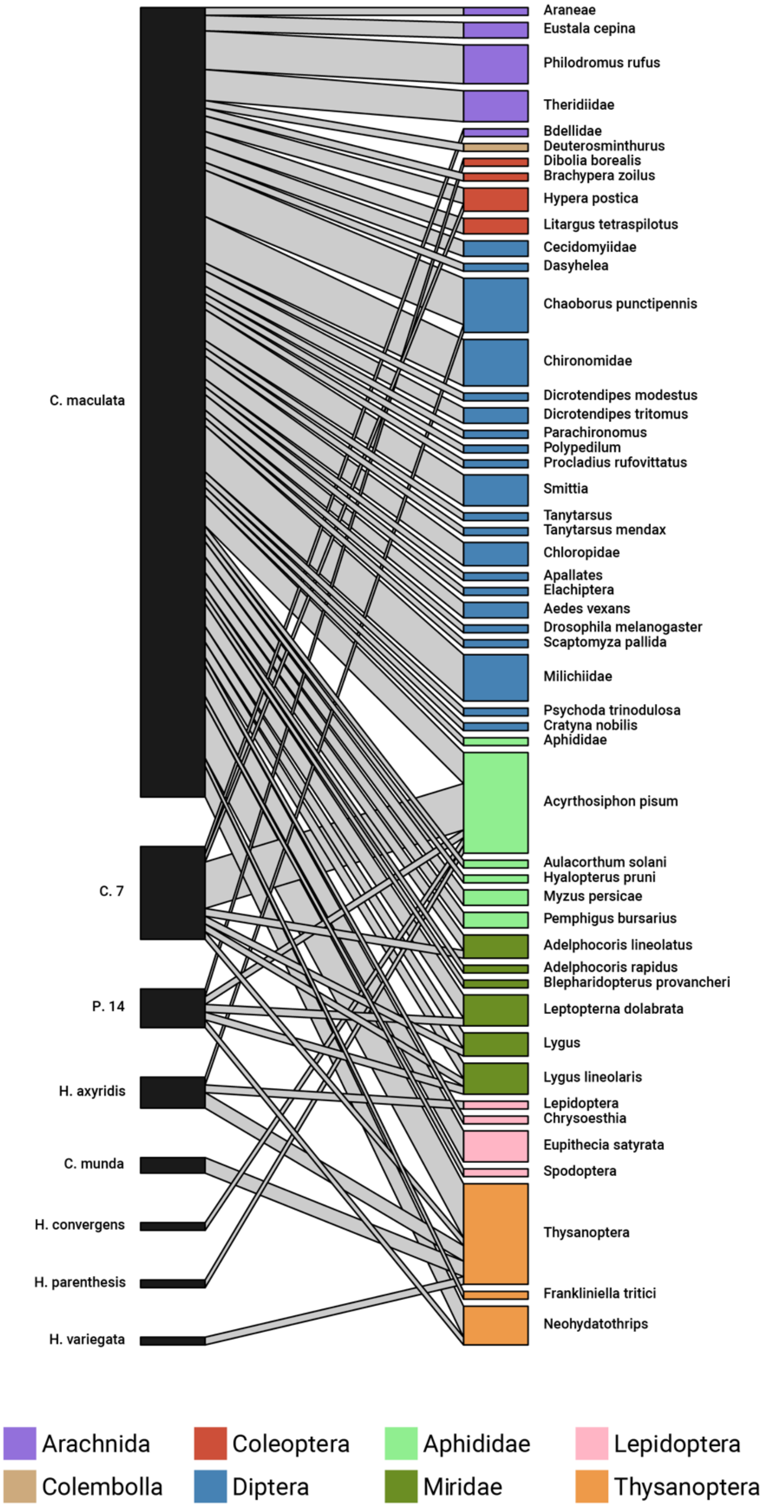

Figure 2.2 Bipartite network diagram of lady beetle-prey trophic relationships from DNA sequencing data. Colors represent arthropod orders of prey taxa, with the exception of hemipterans which are divided into aphids (light green) and mirid bugs (dark green). Labels correspond to the lowest taxonomic level identified.

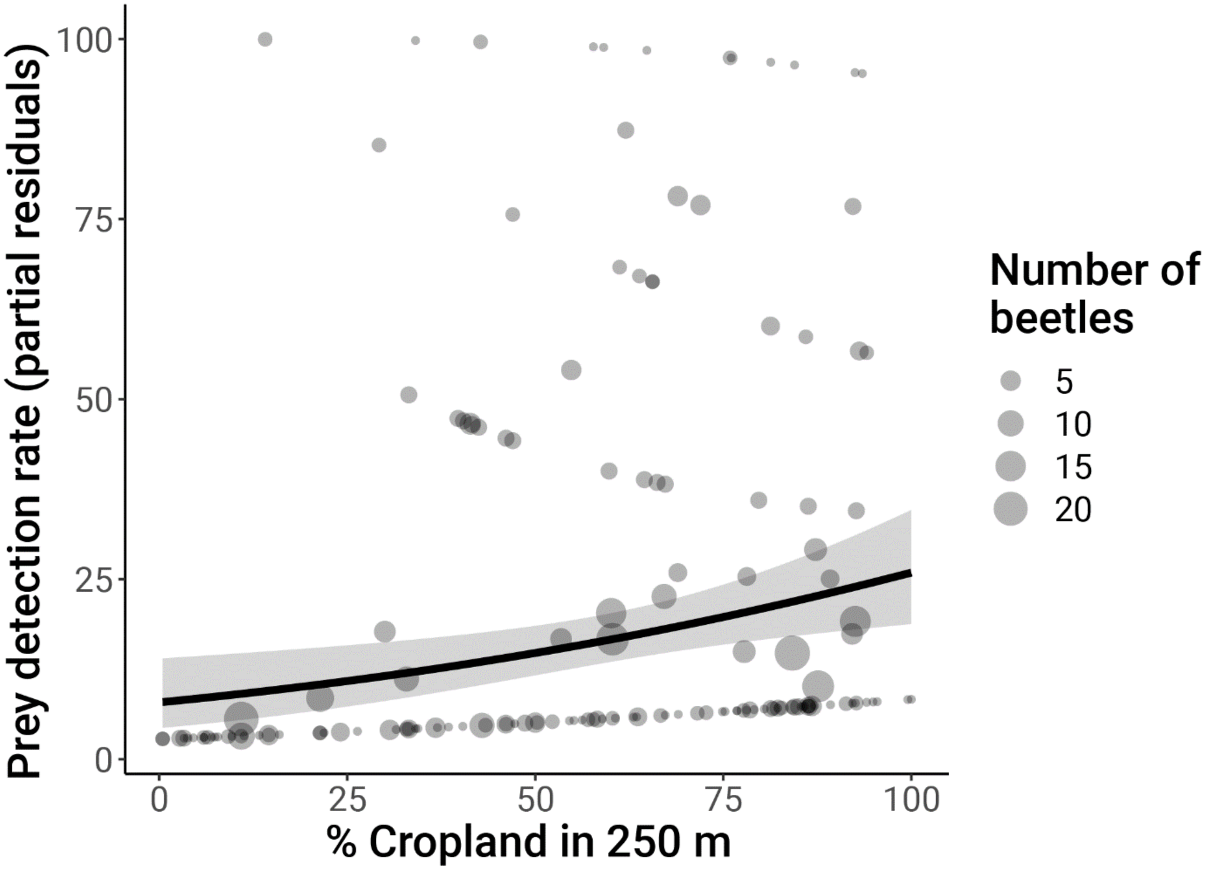

Figure 2.3 Predicted effects of proportion cropland within 250 m of collection sites on prey detection rates. Points are partial residuals averaging over the random effect of site nested within year. Point sizes represent the number of lady beetles sequenced per site. Shaded area depicts 95% confidence interval.

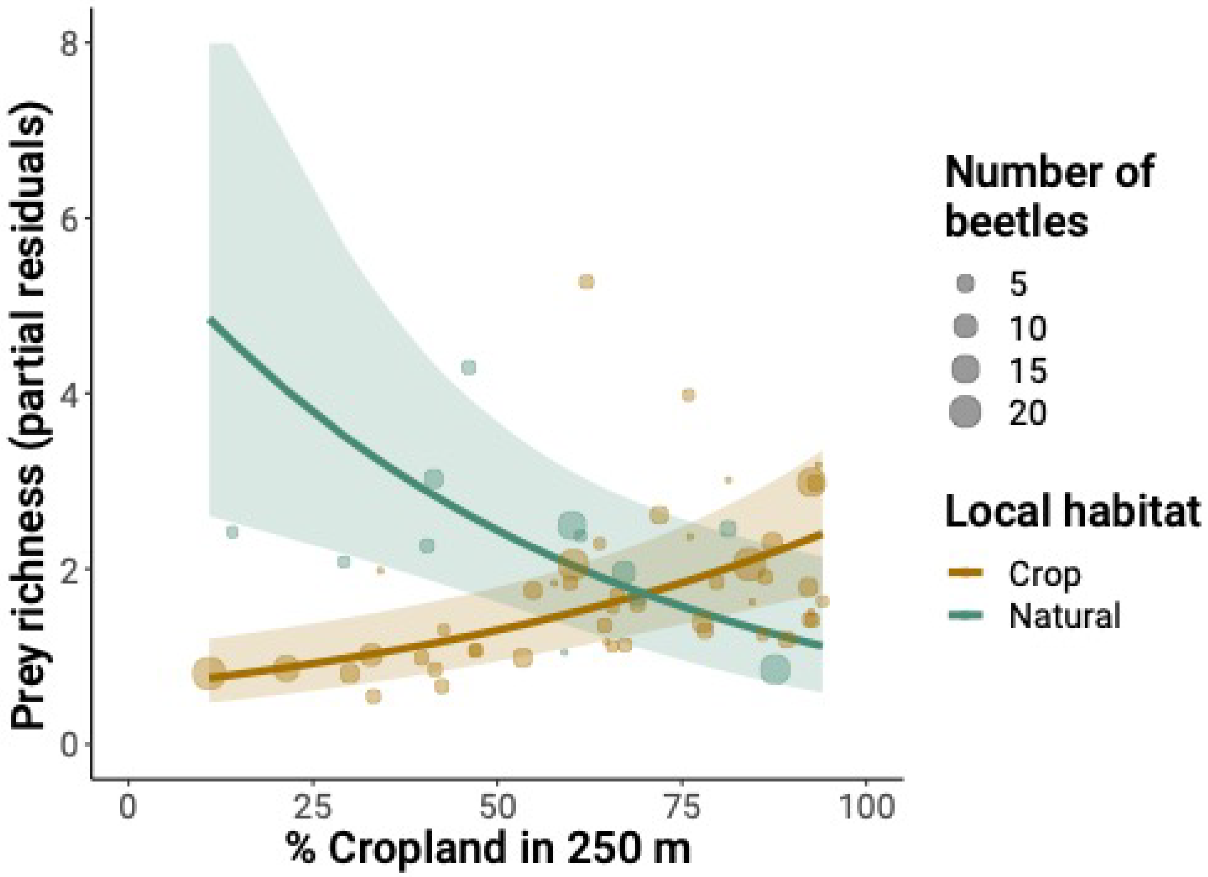

Figure 2.4 Predicted effects of the proportion cropland within 250 m of collection sites on lady beetle prey taxa richness by local habitat type. Points are partial residuals holding landscape diversity at its mean and averaging over random effect of site nested within year. Point sizes represent the number of lady beetles sequenced per site. Colors represent local habitat category. Shaded areas depict 95% confidence intervals.

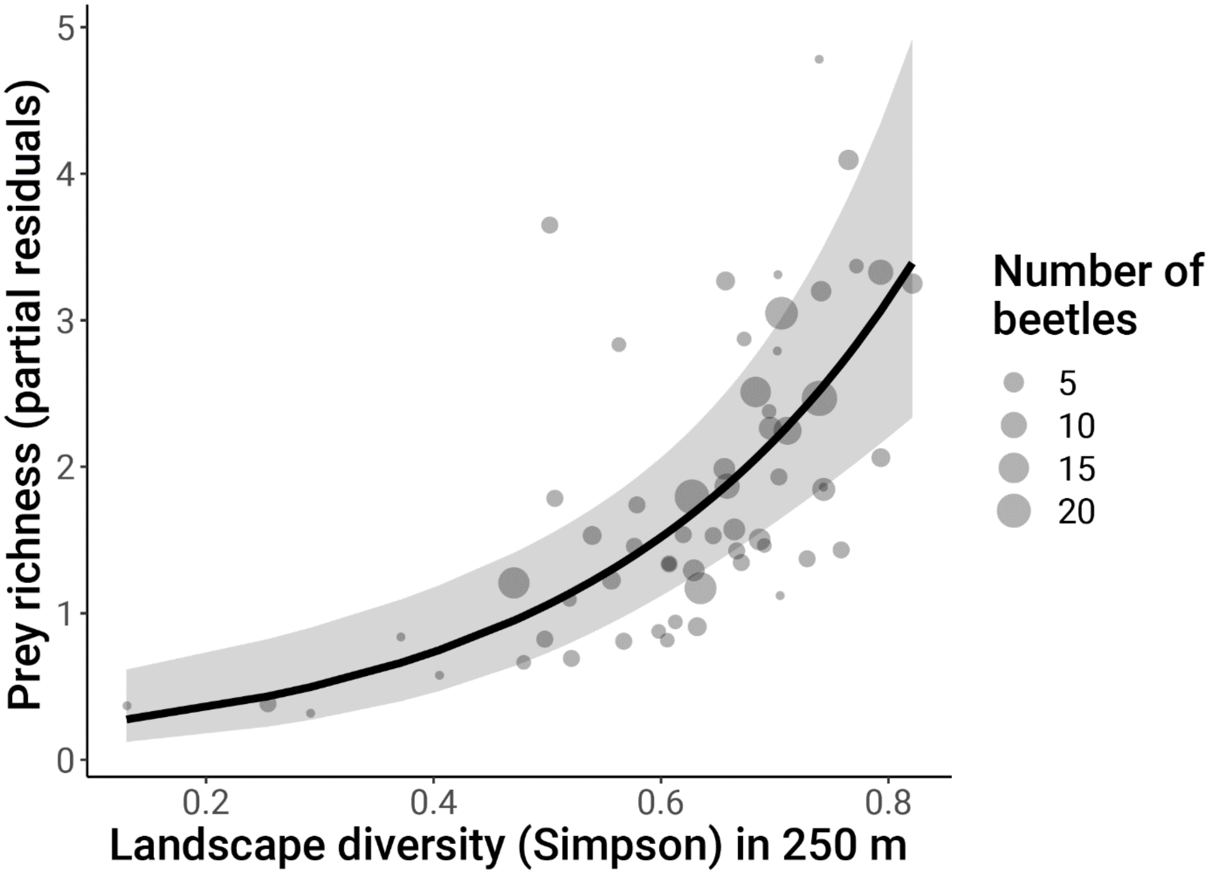

Figure 2.5 Predicted effects of landscape diversity within 250 m of collection sites on lady beetle prey taxa richness. Points are partial residuals, holding proportion cropland at its mean and averaging over local habitat category and the random effect of site nested within year. Point sizes represent the number of lady beetles sequenced per site.

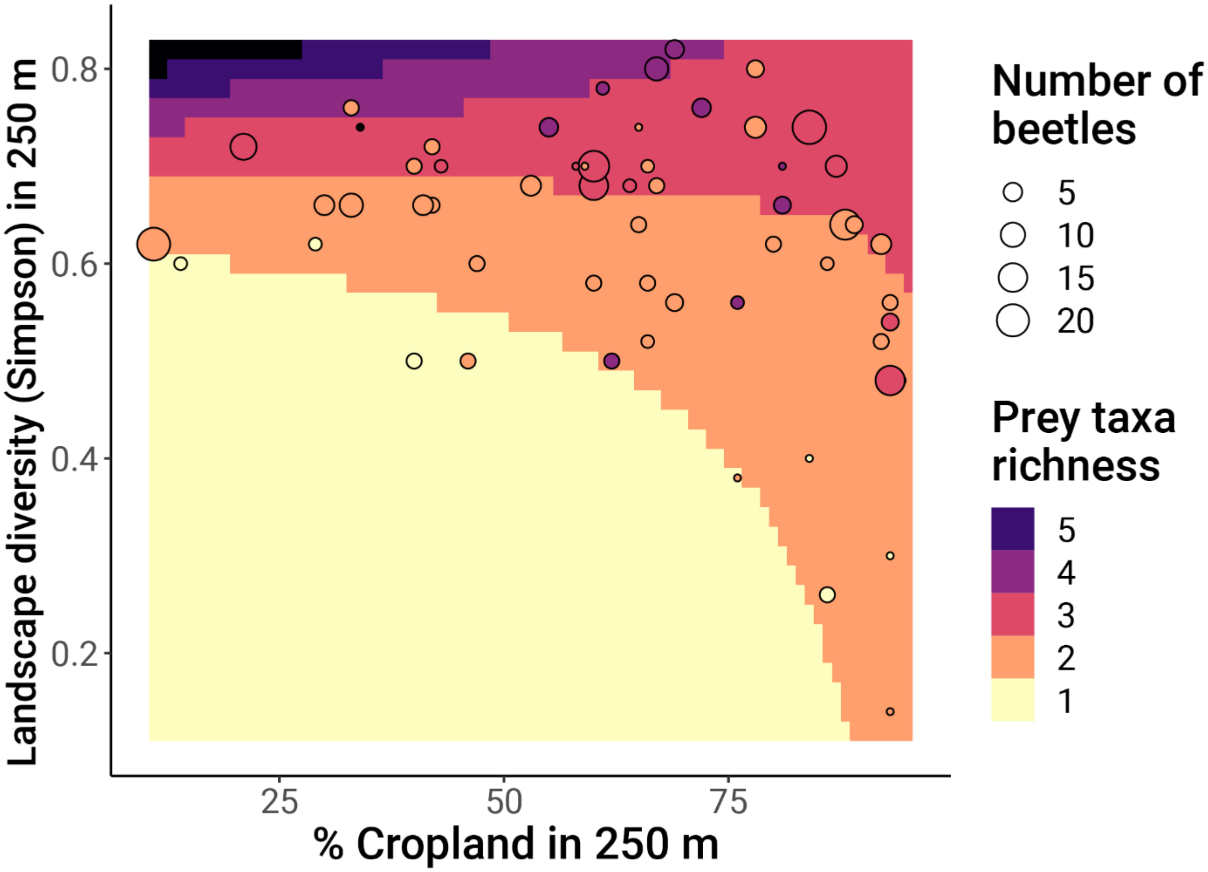

Figure 2.6 Predicted interaction of proportion cropland and landscape diversity within 250 m of collection sites on lady beetle prey taxa richness. Background colors represents model-predicted prey richness. Points represent partial residuals of observed prey richness, averaging over local habitat type and the random effect of site nested within year. Point sizes represent the number of lady beetles sequenced per site.

Chapter 3

High densities of early-season predators promote late-season soybean aphid suppression, but in-field crop temporal diversity has inconsistent effects

Abstract

Crop diversification for natural enemy conservation and pest control has the potential to be an effective strategy for the ecological intensification of agriculture. In particular, managing the temporal diversity of spatially co-occurring crops could result in the earlier recruitment of predators and enhanced pest suppression. In this study, we conducted a three-year experiment using small grains and soybean crops to investigate the effects of two temporal diversification strategies (relay strip intercropping and planting green into cover crops) on aphid and predator populations. We found that larger predator communities earlier in the growing season were associated with lower aphid population growth rates in soybean. However, the impact of diversification treatments on these dynamics was inconsistent, possibly due to management differences across study years and a mismatch between the scales of relevant ecological processes and our experimental manipulations. Research is needed to further clarify underlying mechanisms and optimize other management factors in diversified agroecosystems. This study contributes to understanding of the role of temporal dynamics in predator conservation and pest suppression, and provides valuable insights for the development of successful ecological intensification schemes in agricultural landscapes.

Author contributions Ben Iuliano and Claudio Gratton conceived of the study. Ben Iuliano and Gabriella Stadler led field work and sample processing. Ben Iuliano wrote the first manuscript draft. Claudio Gratton reviewed and contributed to subsequent drafts.

Introduction

Addressing the present biodiversity crisis while meeting demand for agricultural goods will require novel crop management practices that balance insect conservation with pest control. Conventional approaches to the intensification of agriculture typically reduce agrobiodiversity to make agroecosystems easier to manage with external inputs such as chemical insecticides, which replace and erode ecological processes (i.e. predation of pests by natural enemies) that form the basis of crop production (Geiger et al. 2010; Emmerson et al. 2016). The concept of "ecological intensification" has been introduced as an alternative paradigm for the design of cropping systems that enhance biodiversity and ecosystem function on farmland, increase yield, reduce reliance on synthetic inputs, and minimize negative environmental externalities (Bommarco et al. 2013; Kleijn et al. 2019).

Reintroducing and enhancing crop diversity in farm fields is a widely-advocated practice for ecological intensification (Kremen and Miles 2012; Kremen et al. 2012; Ponisio et al. 2015), and insect pest management in particular (Letourneau et al. 2011; Huss et al. 2022). One popular justification is the "enemies hypothesis" (Root 1973), which posits that natural enemies are more abundant and/or kill herbivores at higher rates in diverse systems, reducing their population densities. Yet the mechanisms by which diversification can enhance predator activity and suppress pests, and under what conditions, are highly contextual and remain an area of active scientific inquiry. Initial research on the effects of plant diversity on insect populations (Root 1973; Russell 1989) proposed five mechanism for the enemies hypothesis: 1) alternative food resources (nectar, pollen) for predators, 2) prey refugia, preventing unstable population dynamics, 3) increased nutritional diversity of prey, 4) increased temporal stability of prey, and 5) early enemy recruitment to growing pest populations. Subsequent research has investigated each of these, but the temporal dimensions captured by the latter mechanisms have recently garnered renewed attention (Iuliano and Gratton 2020).

By managing cropping systems so as to influence the temporal diversity of resources for natural enemies, farmers may be able to enhance biological pest control while minimizing the negative effects of plant competition for limiting resources (Letourneau et al. 2011). For example, planting crops with distinct phenologies in the same area may support earlier natural enemy recruitment, retention, and population growth in the early-season crop, ensuring effective pest suppression in the later-season crop (e.g. "apparent competition"; Langer and Hance 2004; Blitzer and Welter 2011). There are several management schemes that may enable such temporal diversification at the field-scale, each with its own ecological characteristics and potential costs and benefits for farmers. Two promising options include relay strip intercropping (Brooker et al. 2015; Li et al. 2020) and "planting green" into cover crops (Reed et al. 2019; Inveninato Carmona et al. 2021). Both of these management systems involve growing two crops in the same field, but differ in the degree of temporal and spatial overlap. In relay strip intercropping, multi-row strips of one crop are planted first, followed by alternating multi-row strips of the second crop at a later date; the first crop is also harvested first, followed by the second crop. In this system, the crops are more spatially segregated but have a longer period of temporal overlap. In green plant cover crop systems, the entire field is planted to the first crop (typically in the preceding fall in temperate regions), the second crop is interseeded between the cover crop rows (in the spring), and the first crop is subsequently terminated (via herbicide, mowing, roller crimping, or grazing). In this system, crops have greater spatial overlap but reduced temporal overlap since the early crop must be terminated for the second crop to establish. In addition to ecological differences, these different systems of crop diversification may be more or less appropriate depending on a farmer's local climate, soil type, equipment, markets, and other agronomic considerations.

Understanding the extent to which crop temporal diversification can contribute to predator conservation and pest suppression, and how this varies by management system, is necessary for the development and implementation of successful ecological intensification schemes. To this end, we designed an experiment to test whether fields planted with two phenologically distinct crops provide temporally complementary prey, increase predator abundance, shift the timing of peak predator abundance earlier in the season, and suppress pests in the later-season crop. In three study years, we planted plots with small grains (spring oats *Avena sativa* or winter wheat *Triticum aestivum*) as an early season crop in different arrangements with soybean (*Glycine max)* as a late season crop. We then measured the responses of aphids and three groups of common generalist natural enemies in the region (lady beetles, lacewings, and hover flies; Costamagna et al. 2008; Gardiner et al. 2009a) throughout the growing season. These crops are typical of annual rotations in the

Midwestern U.S. and have overlapping communities of generalist predators that attack aphids, which can be economically damaging pests in both crop types (Tilmon et al. 2021; Luo et al. 2022). We predicted that phenological patterns (i.e., abundance over time) of aphids and predators would differ between crop types, that plots with small grains would have larger, earlier peaks in predator abundance, and that these would be negatively correlated with subsequent soybean aphid population growth rates.

Methods

Experimental design

Research plots measuring 27 m x 43 m (~0.12 hectares) were established at the University of Wisconsin Arlington Agricultural Research Station Wisconsin, USA (43.295, -89.379) in 2020. In all three years of the study, research plots consisted of four replicates of four treatments each (Table 1). The 16 research plots per year were established randomly in a larger array of 60 plots planted to other field crops (corn, hemp) or perennial vegetation (switchgrass, native grass mix, or native prairie). All plots in the array were separated by ~15 m wide grassy margins (Figure 3.1A).

In each year, treatments consisted of two monocultures and two biculutres (Table 1, Figure 3.1). Soybean was used as the late-season, focal crop in all three years of the study. Because cover crops require seeding in the preceding fall, we were not able to include a cover crop treatment in the first study year (2020). Instead, spring oat was used as the early season crop and the biculture treatments consisted of wide relay strips (9 m wide alternating strips of oats and soybean) and narrow relay strips (2 m wide alternating strips of oats and soybean). In 2021 and 2022, winter wheat was used as the early season crop (planted the preceding fall) and the biculture treatments consisted of relay strips (4.5 m wide alternating strips of wheat and soybean) and a wheat cover crop planted green to soybean. In relay strip plots (all study years), oats or wheat were grown to maturity, allowed to naturally dry down, and harvested mid-summer. In cover crop plots (2021 and 2022 only), wheat was terminated with herbicide (glyphosate) after soybean emergence. All experimental plots were treated with grower-standard fertilizers, herbicides, and fungicides as recommended by research station agronomists. No insecticides were used in experimental plots over the duration of the study.

Insect survey

We surveyed aphids and their generalist insect predators (lady beetles, syrphid flies, and lacewings) weekly between May and August using three sampling methods. First, we conducted counts of aphids on all vegetation within a 0.25 m^2 quadrat at eight sampling points within each plot (Figure 3.1B). In monoculture plots, all eight quadrats consisted of the same vegetation type (oats or soybean in 2020 and wheat or soybean in 2021 and 2022). In relay strip plots (all study years), four quadrats were in the small grains (oats or wheat) and four were in soybean. In cover crop plots (2021 and 2022 only), quadrats contained wheat early in the season, mixed vegetation mid-season, and soybeans late in the season.

Second, we conducted four sweep net samples per plot per date to survey both aphids and predators. Each sample consisted of 25 back-and-forth sweeps using a standard (38 cm diameter) canvas sweep net (BioQuip, Rancho Dominguez, CA). Similar to plant count surveys, all four sweeps occurred in the same vegetation type in monocrop plots, two occurred in each type in strip intercrop plots, and four occurred in single or mixed vegetation type in cover crop plots depending on the time of the growing season. After each sweep sample, bag contents were emptied into a white dishpan (40 cm x 32 cm x 15 cm), and insect predators and aphids were identified and counted in the field. If aphids exceeded 100 individuals per sample, we subsampled counts from one quarter of the dishpan and extrapolated to the full sample. We identified aphids to superfamily Aphidoidea, lady beetle (Coccinellidae) adults and larvae to species, hover fly adults and larvae to family Syrphidae, and lacewings adults and larvae to families Chrysopidae or Hemerobiidae. During periods of the season when little to no vegetation was present (pre-emergence in soybean and post-harvest in wheat), counts from plant surveys and sweep samples were presumed to be zero.

Third, we used yellow sticky card traps (Great Lakes IPM, Vestaburg, MI; Trécé PHEROCON AM no-bait traps or Scentry Multigard traps) mounted ~1.5 m off the ground on green fiberglass gardening stakes to survey flying adult predators. Sticky cards were collected and replaced weekly (except for a few instances where we were unable to sample due to crop management schedule), between weekly plant count and sweep net surveys. Upon collection cards were covered with transparent acetate sheets and stored in a -20 °C freezer until insects could be identified and counted in the lab. We identified adult lady beetles, hover flies, and lacewings as described above for sweep net samples.

Soybean aphid biological control assessment

We evaluated the contribution of predators to soybean aphid suppression in two ways. First, we used data from aphid plant counts on soybean and predators on sticky cards and in sweep samples to correlate peak predator abundance and timing with aphid population growth rates. For each experimental plot in each study year, we calculated the maximum predator abundance over the duration of the sampling period, and the calendar week of this maximum. We then calculated aphid population growth following predator peak as the slope of the correlation between calendar week and the natural logarithm of one plus the mean aphid count per plot (Figure S3.1). Because predators in soybean monoculture plots often did not peak until very late in the season (after which time aphid control is irrelevant), within-plot predator peak was an inappropriate initial time point for calculating and comparing aphid population growth rates. Therefore, we used the mean predator peak across small grain monoculture plots as the initial timepoint for calculating aphid population growth rates (and corresponding predator counts) for these plots. Aphid population growth rates for plots that had fewer than three timepoints (i.e. where predator populations peaked near the end of the sampling period) could not be calculated and were excluded from analysis. Second, in 2020 and 2021 we conducted a predator exclusion experiment in August. We found no relationship of treatment or predator peaks with predation services, and thus include details of this experiment as an appendix (Appendix 3.1).

Statistical analyses

All data handling and statistical analyses were conducted in R (R Core Team 2023) with RStudio (RStudio Team 2023). Statistical models were constructed using the package glmmTMB (Brooks et al. 2017), model assumptions were validated using the DHARMa package (Hartig and Lohse 2022), and contrasts were constructed with emmeans (Lenth et al. 2023). Data were visualized using the packages ggplot2 (Wickham 2016), ggeffects (Lüdecke et al. 2023), and ggpubr (Kassambara 2023).

Due to differences in treatments, management, and sampling period we conducted analyses of aphid and predator phenology separately for each study year. We also analyzed data from each insect sampling method separately. To compare aphid phenologies between early and late season crops, we constructed zero-inflated, generalized linear mixed models of aphid or predator counts using crop type, sampling week, and their interaction as fixed effects, plot nested within treatment as a random effect, and either a Poisson or negative binomial error structure, depending on which best fit each dataset, with a log link function. We excluded data from cover crop plots during the period when grain and soybean vegetation overlapped (late may to early June), as there was no way to distinguish crop types in these samples. We followed the same model structure to estimate predator counts from sweep samples.

Because sticky cards provide a more integrated measure of insect activity across a larger spatial extent (thus making attribution to individual crop types within biculture plots inaccurate), we compared predator counts from sticky cards by treatment rather than by crop type.

To compare predator population peaks across treatments, we used all samples in all vegetation types from both sweep net samples and sticky cards. For each sampling method, we modeled the maximum mean predator abundance per plot and the calendar week of that maximum as a function of treatment in simple linear models with a Gaussian error structure. To test for pairwise differences between treatments, we employed Tukey's HSD to adjust *p*-values for multiple comparisons.

To test the effect of peak predator abundance and timing on soybean aphid population growth rates, we combined data across years to construct separate linear mixed models for each predictor (maximum mean predator abundance and calendar week of the maximum) using each predator sampling method (sweep nets and sticky cards). Because the early season crop species and planting arrangement differed between years, we could not model treatment as a fixed effect. We thus included treatment nested within study year as a random effect to account for non-independence.

Results

Aphid and predator phenology

We counted >15,000 aphids on plants and in sweep samples in 2020, >28,000 in 2021, and >8,000 in 2022. Aphids in oats and wheat included greenbug (*Schizaphis graminum* Rondani), English grain aphid (*Sitobion avenae* Fabricius), and bird cherry-oat aphid (*Rhopalosiphum padi* L.). Aphids in soybean were almost exclusively soybean aphids (*Aphis glycines* Matsumura).

Phenological patterns of aphid abundance differed substantially between crop types and across study years (Figure 3.2). Aphids in small grain crops (oats and wheat) were abundant early in the season (May through late June), after which time they declined. This was especially true in wheat (Figure 3.2F). Soybean aphids were consistently lower than grain aphids during the early season period, and increased over the course of July and August, though the magnitude of this pattern differed among study years. In particular, soybean aphid abundances were much higher in 2020 (Figure 3.2A and B) than in 2021 (Figure 3.2C and D) or 2022 (Figure 3.2 E and F).

We counted 2,725 predators in sweep samples and on sticky cards in 2020, 5,650 in 2021, and 2,789 in 2022. Predators on sticky cards were dominated by hoverflies (68% of counts in 2020, 42% in 2021, 82% in 2022), followed by lady beetles, then lacewings. Predators in sweep samples were predominantly lady beetle adults and larvae (37% of counts in 2020, 76% in 2021, 64% in 2022). The most common lady beetle species across samples were the introduced Asian lady beetle (*Harmonia axyridis* Pallas), seven-spotted lady beetle (*Coccinella septempunctata* L.), and fourteen-spotted lady beetle (*Propylea quatuordecimpunctata* L.).

Predator phenology followed similar patterns as aphids, though the differences between years was more stark (Figure 3.3). In 2020, there were no clear differences between sweep sample counts in oat versus soybean until after oat harvest at the beginning of August, after which point predators in oats declined to zero and predators in soybean continued to increase (Figure 3.3A). In contrast, in 2021 and 2022, wheat sweep sample counts were one to two orders of magnitude higher between June and July than soybean sweep sample counts over the same period (Figure 3.3B and C). After wheat harvest in 2021, predator counts in soybean remained low but were higher than in wheat (Figure 3.3B); no data was collected after wheat harvest in 2022.

Based on sticky card data, treatment type had less clear effects on predator counts, though there were still notable patterns in particular study years at certain points in the growing season (Figure 3.4). In 2020, plots with oats tended to have fewer predators than soybean monoculture plots, particularly in late June and August (Figure 3.4A). In 2021, plots with wheat had substantially higher predators than soybean monocultures in mid-June, but this trend abated thereafter (Figure 3.4B). There were no apparent differences in sticky card predator counts between treatments in 2022 (Figure 3.4C).

Peak predator abundance and timing

The effect of treatment on the maximum predator abundance obtained in a single sampling week (i.e. “predator abundance peak”) varied by sampling year (Figure 3.5). In 2020, soybean monoculture plots attained higher predator abundances than any of the treatments that included oat, which were not statistically different from each other (Figure 3.5A, B). In 2021, wheat monocultures attained the highest predator abundance (Figure 3.5C, D). We found moderate evidence that plots with relay strips had intermediate predator counts (higher than soybean monocultures but lower than wheat monocultures) in sweep samples (Figure 3.5D), but sticky card predator counts were not statistically different from other treatments with soybean (Figure 3.5C). Wheat plots also attained higher predator counts than other treatments in 2022 sweep samples (Figure 3.5F), but not on sticky cards (Figure 3.5E).

The timing of maximum predator abundance (“week of peak predator abundance”) tended to be earlier in plots that included small grains compared to soybean monocultures (Figure 3.6), though there was only strong statistical support for this trend in 2020 sweep samples (Figure 3.6B) and 2021 sticky cards (Figure 3.6C). Predator peaks generally occurred earlier in the season (June-July) in 2021 and 2022 than in 2020 (July-August).

Soybean aphid suppression

Aggregating data across years, we found evidence that both the abundance and timing of plot-level predator peak affected soybean aphid population growth rates (Figure 3.7), though this was not driven by the crop planting treatment. The maximum abundance of predators on sticky cards in a given plot was negatively correlated with subsequent growth rates of soybean aphids (Figure 3.7A, $p < 0.001$). For every additional predator measured on sticky cards (over a one week period) at peak, there was a 9% decrease in aphid population growth rates. Data from sweep samples showed a similar trend, but this had weaker statistical support (Figure 3.7B, $p = 0.097$), though the directionality of the pattern is consistent with that observed with sticky cards.

Earlier predator peak in sweep samples was associated with lower aphid growth rates (Figure 3.7D, $p < 0.001$). For every week earlier the predator peak occurred in a plot, aphid growth rates decreased 6%. However, there was little statistical support for this relationship based on the timing of peak predator counts on sticky cards (Figure 3.7C, $p = 0.532$).

Finally, we found no effect of treatment or predator population counts from sticky cards or sweep samples on BSI estimated from the predator exclusion experiments in 2020 and 2021 (Figure A3.1).

Discussion

Manipulating the temporal dimensions of crop-insect interactions is a promising approach for the successful ecological intensification of agriculture (Welch and Harwood 2014; Iuliano and Gratton 2020). In this study, we sought to test whether two field-scale temporal diversifications schemes—relay strip intercropping and planting green into cover crops—could enhance natural pest control by promoting earlier, larger populations of generalist insect predators. We found evidence that plots attaining higher predator populations earlier in the growing season had lower aphid population growth rates over the remainder of the sampling period, but in-field diversification was an inconsistent driver of these dynamics. These results suggest that to become a viable pest management strategy, temporal diversification needs greater agronomic refinement to ensure reliable pest control benefits.

The importance of early predator arrival for successful pest suppression is well-established in predator-prey population models (Ekbom et al. 1992; van der Werf 1995; Ives and Settle 1997) and empirical biocontrol research (Settle et al. 1996; Costamagna et al. 2015), including studies in soybean (Woltz and Landis 2013). Although we did not directly manipulate the timing of predator arrival in our experiment (e.g. with sequentially removed predator exclusion cages), we were able to take advantage of heterogeneous aphid and predator phenology across plots and study years to show that plots attaining greater predator counts earlier in the growing season tended to have lower (and in some cases negative) aphid population growth rates thereafter. Though the directionality of these relationships was consistent, statistical support depended on predator sampling method, potentially reflecting differences in the predator community and activity captured by sticky cards versus sweep samples (Schmidt et al. 2008; Bannerman et al. 2015). Sticky cards are a temporally integrative measure of only adults, while sweep samples are an instantaneous measure of both adults and larvae. Thus, sticky cards may not accurately reflect predator activity on plants at a given time, possibly explaining the weaker relationship with timing of predator peak. Furthermore, sticky cards are more spatially integrative than sweep samples, with sweep sampling potentially not capturing patchy predator distributions. Greater precision of sticky card counts (Bannerman et al. 2015) may thus explain the clearer relationship between aphid growth rates and peak predator abundances when using this method.

Although we found evidence that earlier, larger predator peaks reduced soybean aphid growth rates, these conditions were not clearly influenced by diversification treatments. While plots with small grains did tend to attain maximum predator abundances slightly earlier in the season than soybean monoculture plots across multiple years and sampling methods, this trend was variable across years and depended on the predator sampling method (sweeps vs. sticky cards).

There are several possible agronomic, ecological, and experimental design explanations for this lack of consistent treatment effect on predators and pest suppression. Differences in early-season crops used between years seemed to have a major effect on the phenology of aphids and predators. Specifically, spring oats (used as the early-season crop in 2020) greened up substantially later and had lower aphid counts than winter wheat (used as the early-season crop in 2021 and 2022). This amounted to reduced opportunity for phenological complementarity between early season prey resources and late season soybean pests which lowered early-season predator counts, and may explain why soybean aphids attained much higher population sizes in 2020. However, because oats were only planted in 2020, the effect of grain crop species and annual environmental conditions are confounded, preventing us from being able to make well-supported inferences about this pattern.

The spatial scale of our experimental manipulation may also have been insufficiently large to isolate the effects of diversification treatments on the activity of highly mobile predators like lady beetles, lacewings, and hoverflies at the scale of the area of the full experiment (~ 25 ha site). Populations of these insects are known to respond to landscape elements at spatial extents upwards of 1 km (Gardiner et al. 2009a, b; Liere et al. 2015; Chapter 1); for comparison, our entire experimental plot array occupied an area of less than ~ 500 x 500 m. Thus, it is plausible that vegetation in and around the plot array—including small grain monoculture treatment plots, but also perennial grass and forb mixes (Werling et al. 2014) and surrounding crop fields and pastures—maintained sufficient levels of early-season prey and functioned as predator sources to soybean, obscuring treatment differences at the plot level. Indeed, a large-scale landscape study in the region demonstrated that the presence of a greater proportion of alternative crop fields (such as small grains and alfalfa) within 1.5 km was associated with reduced aphid abundance in soybean fields (Stack Whitney et al. 2016). The fact that soybean aphid populations never reached economic thresholds of 250 aphids per plant (Ragsdale et al. 2007) also indicates that aphids may have been sufficiently controlled in this landscape. All together, this suggests that ensuring sufficient temporal overlap of early and late season crops at a landscape scale (i.e., across multiple fields and farms) may be more important for resource tracking by mobile predators than engineering fine-grained spatial overlap within a field or farm.

Relay strip intercropping and planting green into cover crops are novel cropping systems in U.S. agroecosystems, and more research is needed to understand how to best manage them for multiple agroecosystem functions. A recent meta-analysis by Li et al. (2020) showed that across the globe, relay strips are the intercropping scheme with the highest yield gains relative to monocultures, particularly in maize-based systems with high fertilizer inputs in China. Future studies could evaluate the contribution of pest and enemy dynamics to yield gains, and explore this production syndrome with different crop combinations and in other parts of the world. "Planting green" is a strategy that has only recently begun to receive attention in agricultural research, and shows some early promise for reducing gastropod pests through bottom-up dilution effects (Reed et al. 2019; Le Gall et al. 2022). More research is needed to understand potential consequences for insect populations.

The utility of temporal diversification for pest management will also depend on the economic thresholds for the particular pests and crops involved. In this system described here, economic thresholds for spring grain crops are relatively high, especially if they are used for dairy forage rather than human consumption (Chapter 4), enabling the buildup of prey populations and early recruitment of natural enemies. This may not be true in all cropping systems, and farmers will need to balance potential losses from pest damage with the benefits from natural enemies in subsequent crops. Overall, our study suggests that temporal diversification could be a promising direction for ecological pest management when it results in early arrival of large predator populations to crop fields. Yet designing cropping systems that consistently attain such outcomes without compromising other aspects of the production system will require further agronomic refinement. Our study was not designed to evaluate yield outcomes, but anecdotal observations in the field suggest that mixed cropping systems in experimental plots were associated with greater weed pressure and reduced crop growth. Collaboration with multidisciplinary agricultural scientists to balance other dimensions of agroecosystem management (weeds, nutrients, harvesting techniques, etc.) will be necessary, including new or modified equipment designed for diversified cropping systems (Bybee-Finley and Ryan 2018).

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Tables

Table 3.1 Experimental treatments, key management dates and sampling schedule across three study years.

	Treatment	Planting date	Harvest/termination	Sampling period
2020	Spring oat monoculture	1 May 2020	5 August 2020	Insect Surveys Start: 8 June 2020 End: 20 August 2020
	Soybean monoculture	1 May 2020	October 2020	
	Wide relay strips (9 m)	1 May 2020	5 August 2020 (oats) October 2020 (soybean)	Predator exclusion experiment Start: 11 August 2020 End: 18 August 2020
	Narrow relay strips (2 m)	1 May 2020	5 August 2020 (oats) October 2020 (soybean)	
2021	Winter wheat monoculture	9 October 2020	5 August 2021	Insect Surveys Start: 9 May 2021 End: 28 August 2021
	Soybean monoculture	12 May 2021	October 2021	
	Relay strips (4.5 m)	9 October 2020 (wheat) 12 May 2021 (soybean)	5 August 2021 (wheat) October 2021 (soybean)	Predator exclusion experiment Start: 12 August 2021 End: 16 August 2021
	Cover crop	9 October 2020 (wheat) 12 May 2021 (soybean)	3 June 2021 (wheat) October 2021 (soybean)	
2022	Winter wheat monoculture	19 October 2021	29 July 2022 (wheat)	Insect Surveys Start: 7 May 2021 End: 28 July 2021
	Soybean monoculture	12 May 2022	October 2022 (soybean)	
	Relay strips (4.5 m)	19 October 2021 (wheat) 12 May 2022 (soybean)	29 July 2022 (wheat) October 2022 (soybean)	Predator exclusion experiment N/A
	Cover crop	19 October 2021 (wheat) 12 May 2022 (soybean)	24 May 2022 (wheat) October 2022 (soybean)	

Figures

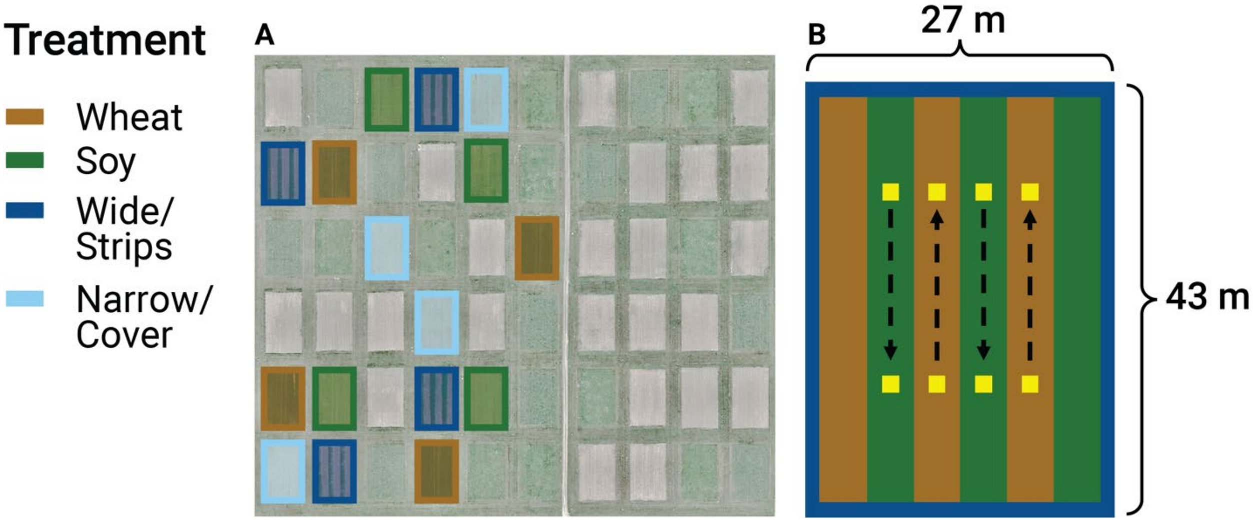

Figure 3.1 Example experimental plot map from 2022. A shows the arrangement of 4 replicates of 4 treatments (indicated by colored borders) embedded in a 60 plot grid. The satellite image was taken in early June, after wheat in cover crop plots had been terminated but before substantial soybean growth. B depicts the sampling scheme in an example strip relay crop plot. Yellow squares represent sticky card and plant count sampling points. Dotted lines with arrows represent sweep net transects.

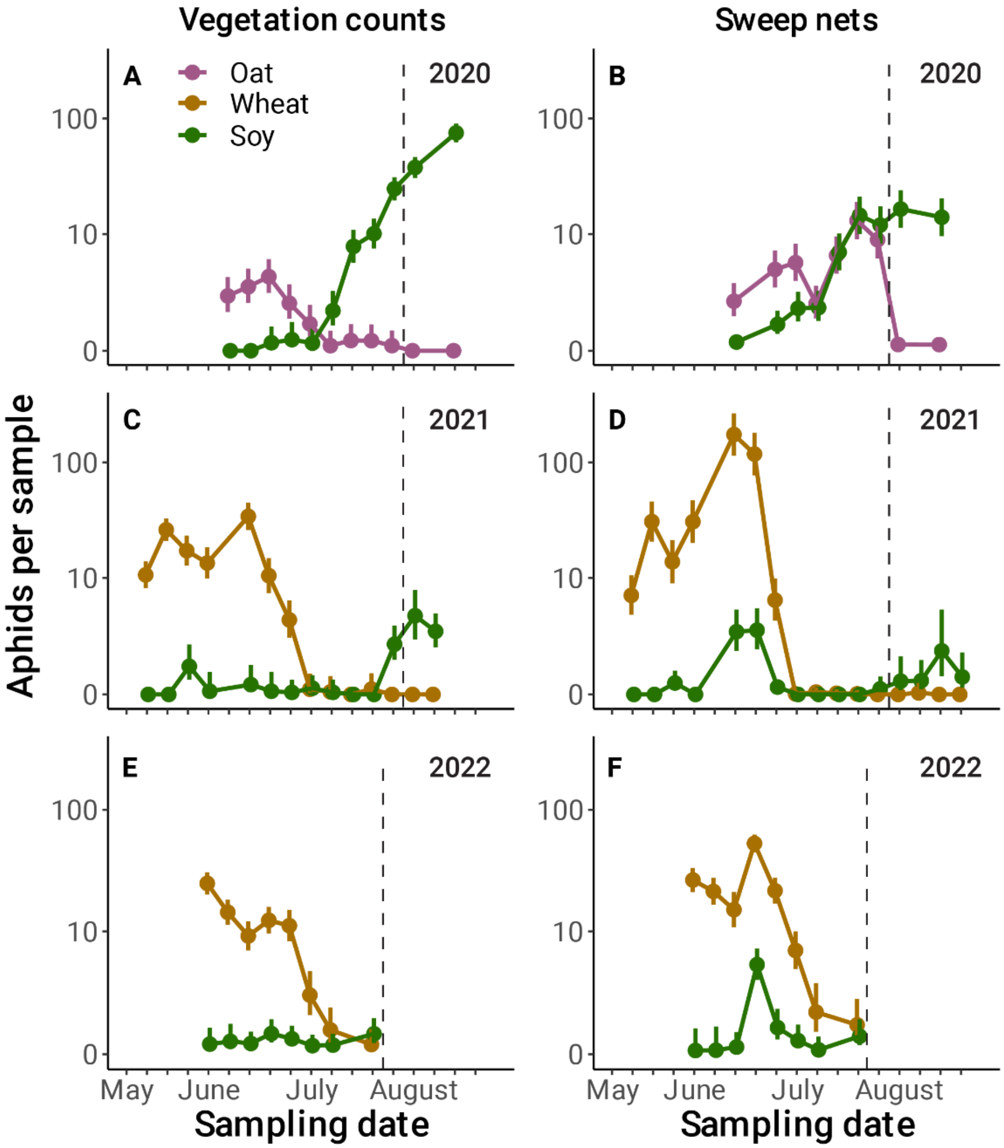

Figure 3.2 Aphid phenology by crop type across three study years. Points are estimated means from a zero-inflated model of the effect of crop type and sampling week on aphid counts, with plot as a random effect. Error bars show 95% confidence intervals. Vertical line represents timing of small grain harvest. Rows correspond to sampling years (2020, A and B; 2021, C and D; 2022, E and F). Panels in the left hand column (A, C, and E) show aphid counts from vegetation survey, and panels in the right hand column (B, D, and F) show counts from sweep netting. Note the y axis is on a logarithmic scale.

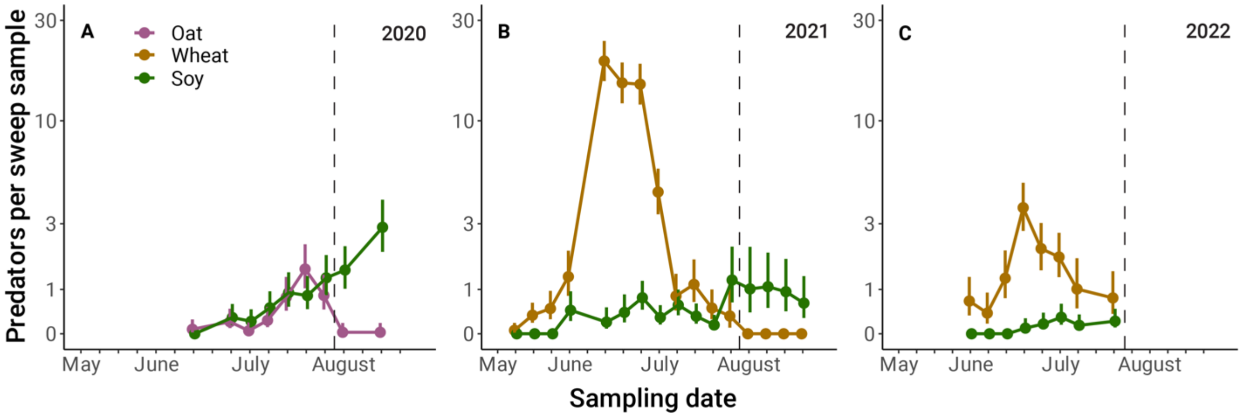

Figure 3.3 Predator phenology in 100 sweep samples by crop type across three study years (A) 2020, (B) 2021, and (C), 2022. Points are estimated means from a zero-inflated model of the effect of crop type and sampling week on predator counts, with sampling point nested within plot as a random effect. Error bars show 95% confidence intervals. Vertical line represents timing of small grain harvest. Note the y axis is on a logarithmic scale.

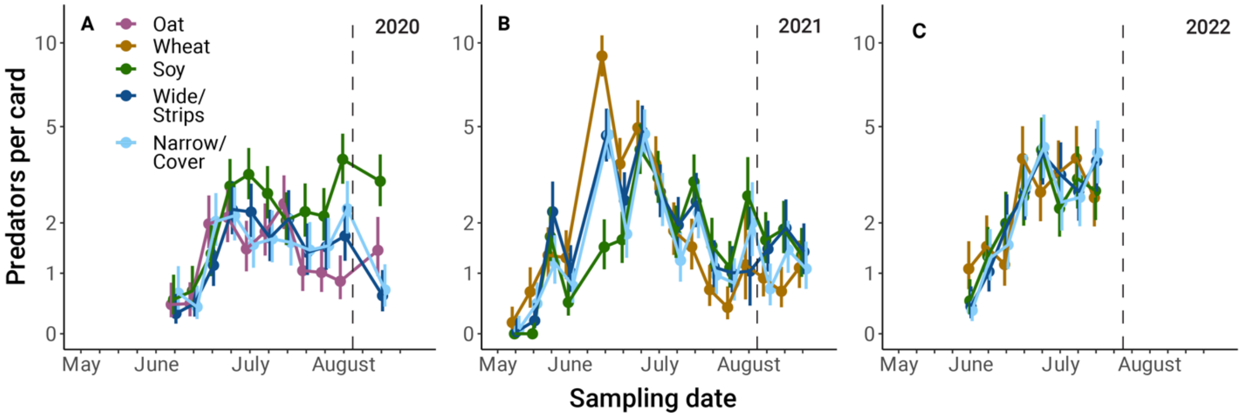

Figure 3.4 Predator phenology on sticky cards by treatment across three study years (A) 2020, (B) 2021, (C) 2022. Points are estimated means from a zero-inflated model of the effect of crop type and sampling week on predator counts, with sampling point nested within plot as a random effect. Error bars show 95% confidence intervals. Vertical line represents timing of small grain harvest. Note the y axis is on a logarithmic scale.

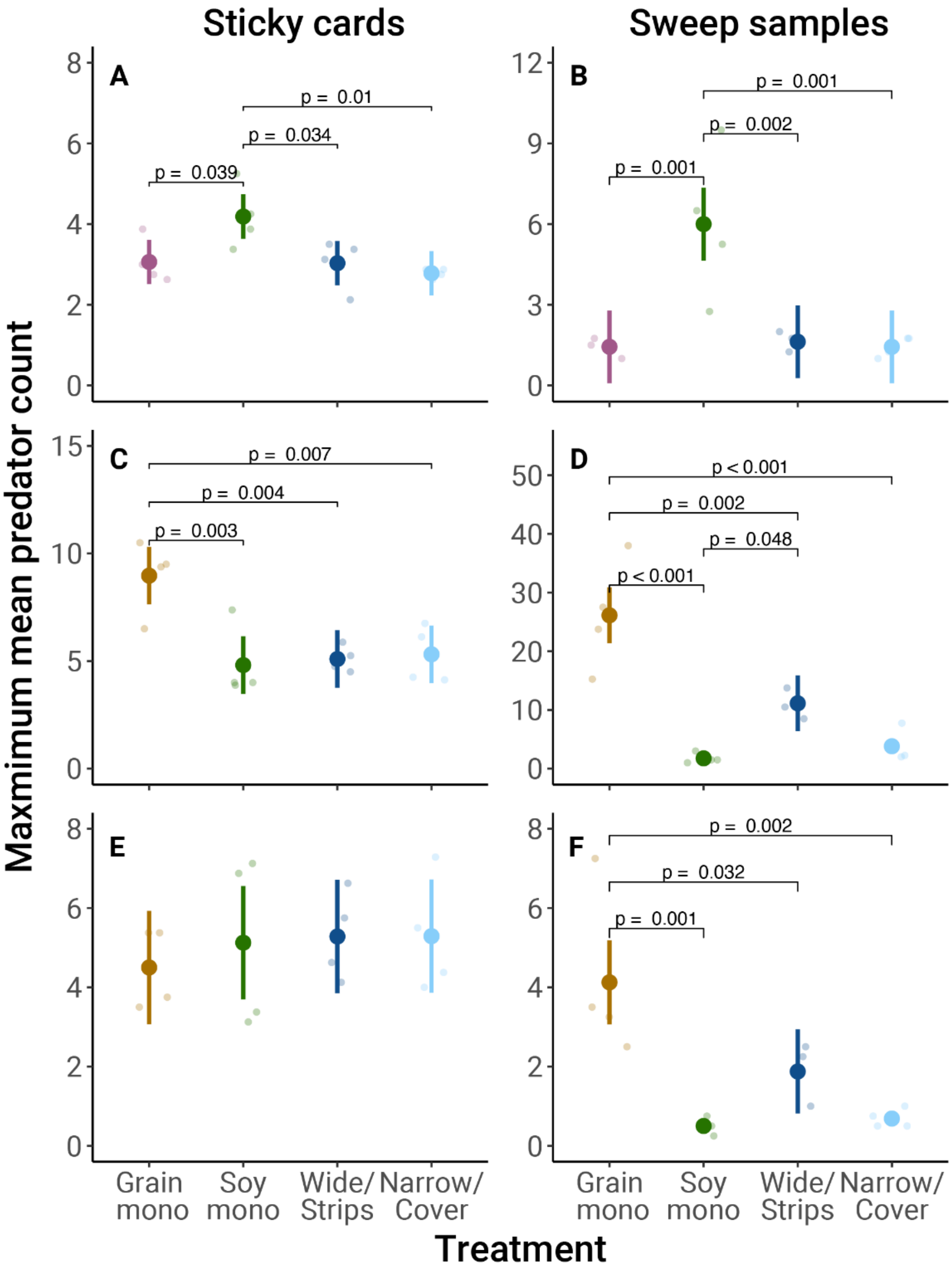

Figure 3.5 Effect of treatment on the maximum predator abundance per plot attained in a single week over the sampling period in three study years. Large, solid points show means and error bars show 95% confidence intervals. Small, transparent points are mean values per plot in the sampling week of maximum predator abundance for that plot. Colors indicate treatment. Rows correspond to sampling years (2020, A and B; 2021, C and D; 2022, E and F). Panels in the left hand column (A, C, and E) show mean predator counts from sticky cards, and panels in the right hand column (B, D, and F) show mean counts from sweep netting. Tukey-adjusted *p*-values < 0.05 for pairwise comparisons are shown.

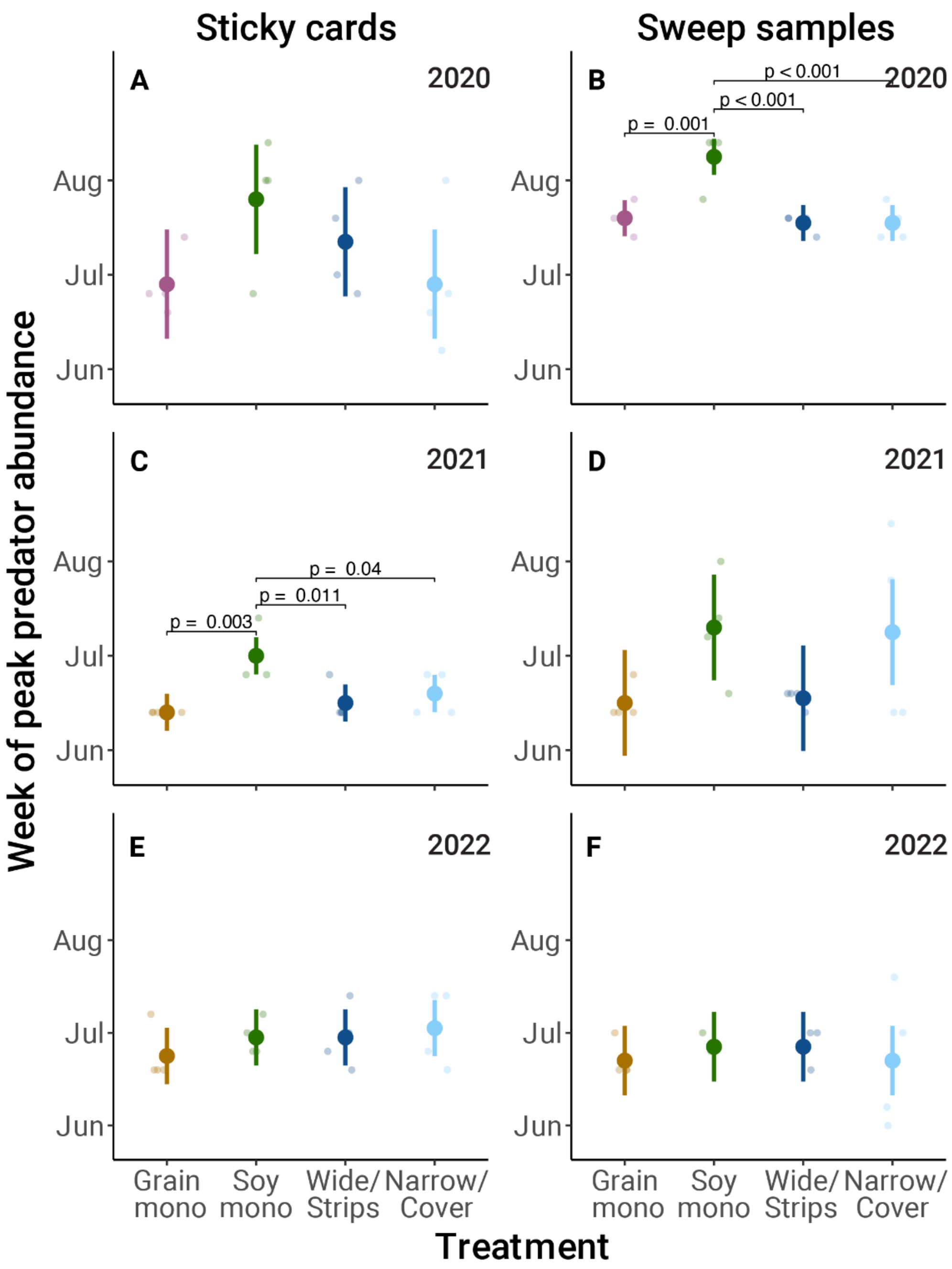

Figure 3.6 Effect of treatment on the week of maximum predator abundance per plot attained over the sampling period in three study years. Large, solid points show means and error bars show 95% confidence intervals. Small, transparent points are the sampling week of maximum mean predator abundance per plot. Colors indicate treatment. Rows correspond to sampling years (2020, A and B; 2021, C and D; 2022, E and F). Panels in the left hand column (A, C, and E) show the week of maximum predator counts on sticky cards, and panels in the right hand column (B, D, and F) show the week of maximum predator counts in sweep nets. Tukey-adjusted *p*-values < 0.05 for all pairwise comparisons are shown.

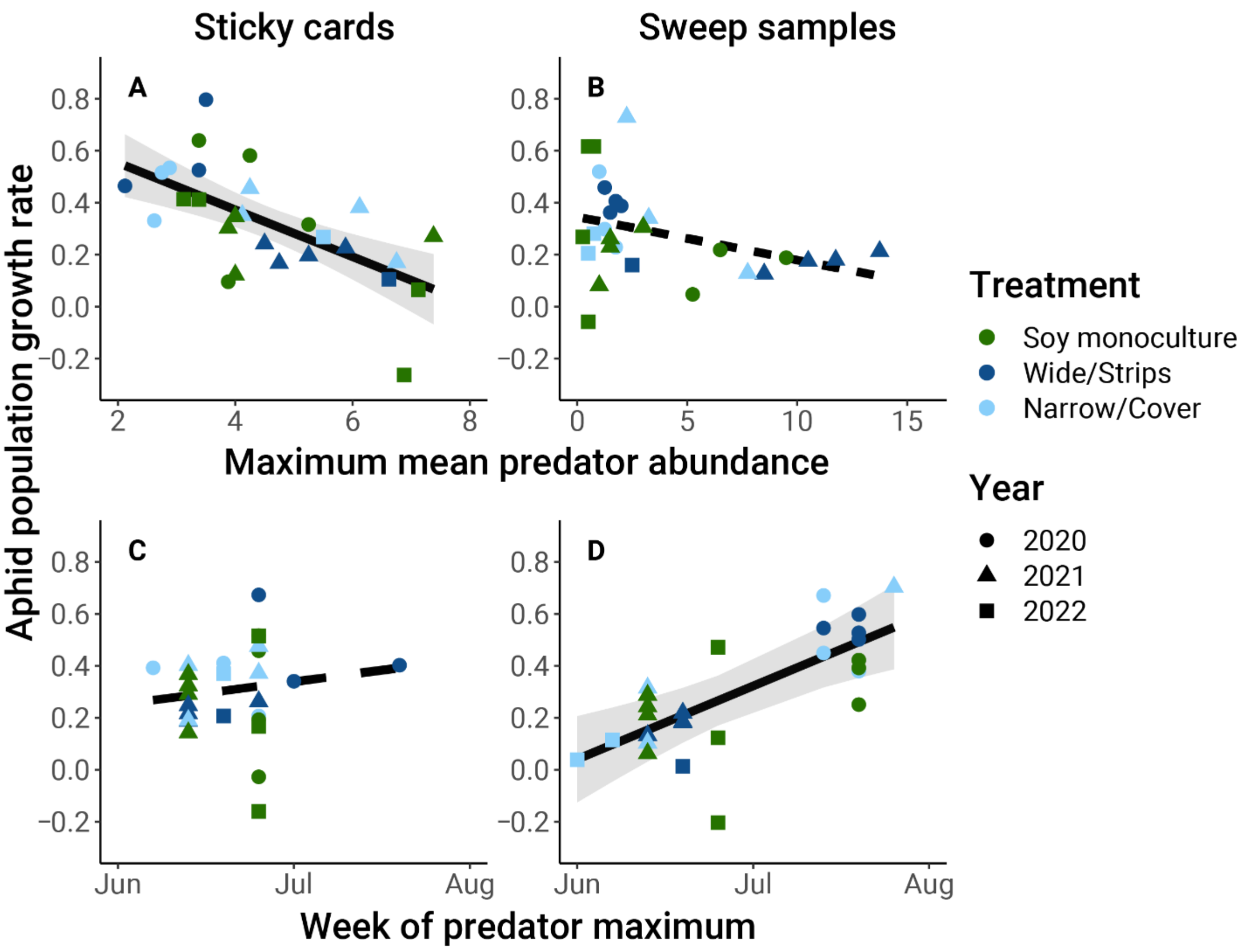

Figure 3.7 Plot-level soybean aphid population growth rate by predator population peak. Top panels (A, B) show the effect of maximum mean predator abundance; bottom panels (C, D) show the effect of the timing (calendar week) of maximum abundance. Left panels (A, C) are based on predator data from sticky cards; right panels (B, D) are based on predator data from sweep net samples. Point colors indicate plot treatments and shapes indicate study year. Solid lines represent relationships with moderate to strong statistical support ($p < 0.05$) and shaded areas depict 95% confidence intervals; dotted lines represent relationships with weak statistical support ($p > 0.05$).

Supplementary material

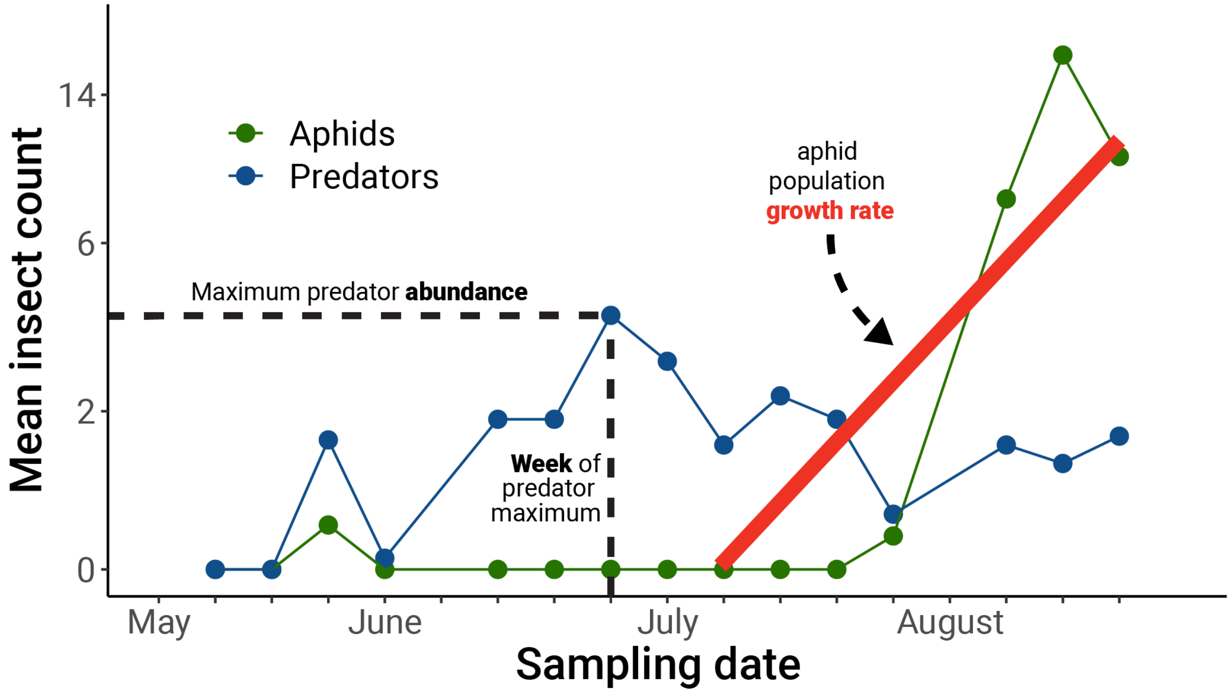

Figure S3.1 Method for calculating peak predator abundance, timing, and subsequent aphid population growth rates. Figure depicts aphid (green) and predator (blue) phenology in a single experimental plot over the course of the sampling period. Points are averaged counts across all subsamples (sweep net samples for aphids and sticky card samples for predators) at a given calendar week. The week of maximum predator abundance within the plot was used as t_0 to calculate plot-scale aphid population growth rates, defined as the slope of the line of best fit (red line) for points between t_0 and the end of the sampling period.

Appendix 3.1 – Predator exclusion experiment

In 2020 and 2021 we conducted a predator exclusion experiment to measure biological control services. In each plot with soybean, we infested four pairs of soybean trifoliate leaves with 10 field-collected soybean aphids each. All other insects were removed from the leaves, and one trifoliate per pair was covered with a mesh bag to exclude predators. We tied mesh around the base of uncovered trifoliates as a control. We then returned the following week (7 days in 2020 and 4 days in 2021) and counted the aphids on covered and uncovered leaves. We calculated a biocontrol service index (BSI) per pair (n=4 pairs per plot) as the number of aphids on the covered trifolate minus the number of aphids on the uncovered trifoliate, divided by the number of aphids on the covered leaves:

$$\mathrm{BSI} = \frac{\mathrm{Aphids}_{\mathrm{bagged}} - \mathrm{Aphids}_{\mathrm{open}}}{\mathrm{Aphids}_{\mathrm{bagged}}}$$

Pairs with leaves that had yellowed or with negative BSI values were excluded from analysis.

To compare BSI between treatments in 2020 and 2021, we modeled BSI calculated from each soybean trifoliate pair with treatment as a fixed effect and plot as a random effect (to account for non-independence of multiple pairs from the same plot) and a gaussian structure.

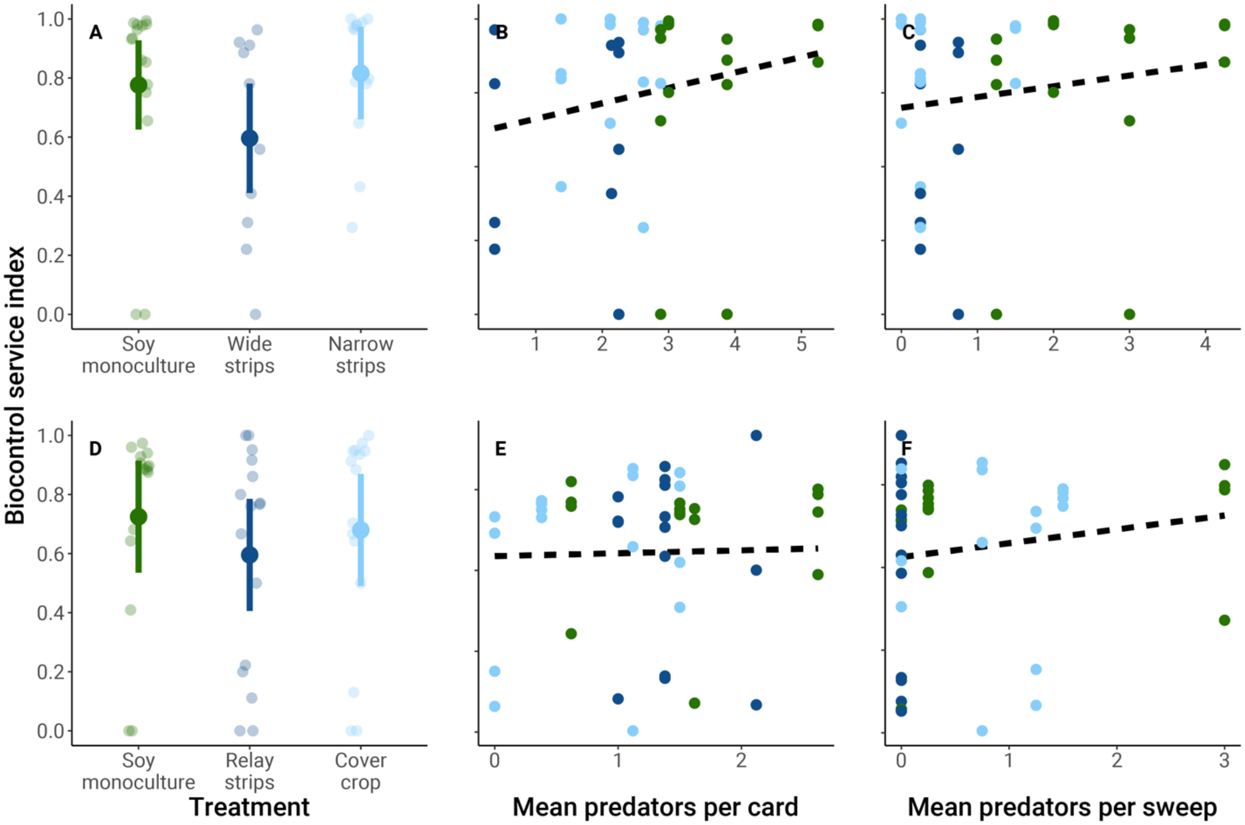

Figure A3.1 Biocontrol service index (BSI) by treatment and predator abundance. Top panels (A-C) show data from 2020, bottom panels (D-F) show data from 2021. Columns show the effect of plot treatment (A, D), contemporaneous plot-level mean predator counts on sticky cards (B, E) and in sweep samples (C, F) on BSI. Small points show BSI values for pairs of covered and uncovered soybean leaf trifoliates infested with soybean. Large points are means from linear mixed models with plot as a random effect. Dotted lines are estimated regression lines; all $p > 0.05$.

Chapter 4

No farm is an island: constrained choice, landscape thinking, and ecological insect management among Wisconsin farmers

Abstract

Agriculture has long struggled to reconcile production with biodiversity conservation. Industrial farming practices that erode structural complexity within crop fields and across entire landscapes, as well as widespread pesticide use, have resulted in declining insect abundance and diversity globally. Recognition of socio-environmental consequences have spurred alternative pest management paradigms such as integrated pest management (IPM) and conservation biological control (CBC), which emphasize ecology as the scientific foundation for a sustainable agriculture. However, adoption of these approaches at scales large enough to impact biodiversity has been slow, particularly in industrialized countries. Landscape-scale management is an integral component of ecological agriculture, making pest control and biodiversity conservation collective problems that require coordination among multiple stakeholders. The extent to which farmers recognize and act upon this perspective is not well studied. Through literature synthesis and a case study of Southern Wisconsin, I analyze factors shaping farmer adoption of insect and landscape management practices through the lens of constrained choice. I argue that multiple overlapping institutions (social networks, market forces, science and technology, and political-legal systems) co-produce farmer behaviors and landscape structure, largely to the detriment of ecological pest control and biodiversity. Wisconsin farmers' entomological concerns largely overlook beneficial insect species and eschew landscape thinking. Ultimately, slowing agricultural drivers of insect biodiversity declines will likely require large-scale coordination and political-economic change.

Author contributions Ben Iuliano conceived of the study, conducted interviews and analysis, and wrote the manuscript.

Introduction

Reconciling production with biodiversity conservation is not a new challenge for agriculture. With the publication of *Silent Spring* in the mid-twentieth century, Rachel Carson sparked widespread scientific and public concern about how industrial farming practices—in particular the growing reliance on synthetic chemical pesticides—were compromising public health and ecological integrity (Carson 1962). Remarkably similar concerns persist today. In addition to pesticides, the loss of structural complexity within individual crop fields and across entire landscapes has also been linked to shifting patterns of insect life. In particular, widespread pesticide use and landscape simplification have been implicated as major drivers of precipitous declines in the abundance and diversity of insects in many parts of the world (Wagner 2020; Wagner et al. 2021; Goulson 2021). Furthermore, the syndromes of production (Vandermeer 1997; Vandermeer and Perfecto 2012) typical of contemporary industrial agriculture tend toward conditions in which pests can thrive while beneficial species suffer (Bakker et al. 2020; Nicholson and Williams 2021).

Scientists from a variety of disciplines have long advocated for alternative paradigms for interacting with agricultural insects, beginning with the move from “pest control” to “integrated control” and “pest management” in the first half of the twentieth century (Stern et al. 1959), culminating in “integrated pest management” (IPM; Kogan 1998; more recently Integrated Pest and Pollinator Management, IPPM; Egan et al. 2020; Lundin et al. 2021) and conservation biological control (CBC; Landis et al. 2000; Shields et al. 2019). These latter approaches emphasize that the discipline of ecology, as opposed to chemistry or agronomy, should be the scientific foundation for a more sustainable agriculture (Palladino 1996; Tittonell 2014). Rather than focus narrowly on eliminating pests, they advocate for managing the entire community of insects that may help (predators, pollinators) or hinder crop production.

While CBC and IPM have gained individual and (occasionally) institutional support, farmers—particularly in the industrial production systems of the United States and Europe—have been slow to adopt them at scales large enough to matter for biodiversity (Chaplin-Kramer et al. 2019). In particular, researchers have repeatedly demonstrated that the structure of the landscape surrounding crop fields affects the suppression of pests and retention of beneficial insects on farms. While the strength and direction of these relationships are highly context-dependent (Karp et al. 2018; Alexandridis et al. 2022), the landscape frequently matters as much as or more than in-field conditions. Thus, landscape-scale or "area-wide" management (Vreysen et al. 2007) is an integral component of ecologically-based agriculture (Haan et al. 2021; Tscharntke et al. 2021). This makes both pest management as well as biodiversity conservation inherently collective problems that require coordination among multiple farmers and other people that share agricultural landscapes. To what extent farmers and policymakers recognize and act upon this perspective—their degree of "landscape thinking"—is not well studied, particularly on highly-capitalized farms in the U.S.

In this chapter, I draw from rural sociology, political ecology, and science and technology studies (STS) to analyze farmers' adoption of insect and landscape management practices. Through literature synthesis and a case study of Southern Wisconsin, I argue that particular social, structural, and ideological conditions constrain farmers' ability to conceptualize and implement ecological insect management approaches, particularly at scales larger than their own farm (i.e. the landscape). The concept of "constrained choice" (Hendrickson and James 2005; Baur 2020) serves as a key starting point for my analysis. I begin with a review of the disparate literature on drivers of farm management practices from individual to institutional levels, with particular attention to insects and biodiversity. I then apply these conceptual frames to data from semi-structured interviews with farmers to evaluate potential constraints on agroecological landscape design. I show that Wisconsin farmers' entomological concerns largely overlook beneficial insect species and eschew landscape thinking. Ultimately, while individual farmers are occasionally able to evade constraints on ecological management, slowing agricultural drivers of insect biodiversity declines will likely require large-scale coordination and political-economic change.

From farmer decisions to constrained choice

A vast body of scholarly work attempts to answer why farmers engage in particular land management practices and under what conditions they might change. This work spans a range of epistemological and methodological approaches, including quantitative (Knowler and Bradshaw 2007; Baumgart-Getz et al. 2012; Prokopy et al. 2019; Lu et al. 2022) and qualitative (Reimer et al. 2012; Baur 2020; Esquivel et al. 2021; Carlisle et al. 2022) research in rural and environmental sociology, agricultural economics, geography, and more. Here, I focus on work that is particularly relevant to the issues of pest management and biodiversity conservation, at the scale of individual farm fields to shared landscapes.

The bulk of the quantitative social science literature on farmer adoption of agricultural conservation practices is based on survey data, within which researchers look for attitudinal (e.g. environmentalism, risk aversion) and/or demographic (e.g. farm size, farmer age) correlates of particular intentions and behaviors (e.g. planting cover crops, participation in government programs). Multiple reviews and meta-analyses have found highly variable and context-dependent reasons for conservation practice adoption, but past adoption of related practices and positive experiences with conservation programs tend to be some of the strongest predictors (Prokopy et al. 2019). While environmentalist attitudes and awareness of the environmental impacts of agriculture are frequently positively associated with farmers' intent to adopt conservation practices, associations with actual adoption are weaker (Lu et al. 2022). Furthermore, most of the adoption literature is concerned with practices related to soil and nutrient management, not biodiversity; In one of the most comprehensive reviews to date of conservation practice adoption by U.S. farmers, just 7% of the studies considered pest control, and less than 1% considered habitat management (Prokopy et al. 2019; but see Dixon et al. 2022).

Of the few studies that have been conducted on farmer knowledge of beneficial insects and their services, the vast majority occurred outside of countries with highly-capitalized, industrial production systems (Rawluk and Saunders 2019; but see subsequent work from Hevia et al. 2020; Maas et al. 2021; Busse et al. 2021; Osterman et al. 2021). Even fewer studies have connected farmer knowledge about insects to landscape-scale processes, despite the large body of ecological work on these relationships. In one notable exception, Salliou and Barnaud (2017) examined French apple growers' mental models of "the landscape" and "natural enemies" as resources or liabilities for crop production. They found that while natural enemies were understood as public goods by many growers, unfarmed areas of the landscape were almost universally perceived as a source of pests. Furthermore, farmer-driven habitat management innovations tended toward individualism (e.g. placing nets to enhance augmentative release of natural enemies) rather than collectivism (e.g. coordinated landscape management). Missing from this analysis are the social and structural conditions in which farmer decision making occurs.

In sum, while the literature examining farmers' knowledge, perceptions, attitudes, and practices provides valuable insights about insect and landscape management, its individualistic framing cannot adequately capture the larger-scale forces that shape farmers' behaviors and, accordingly, agricultural landscape structure. An important theoretical intervention that helps bridge this gap, and may explain the observed discrepancy between intention and adoption of ecological management, is the concept of "constrained choice," first described in the context of agriculture by Hendrickson and James (2005, 2016). They show how industrialization and concentration in the agri-food sector narrows the scope of both available inputs (plant and animal varieties, equipment, etc.) as well as possible outputs (i.e. markets for farm products), leading to loss of knowledge, skills, agrobiodiversity, and the ability to make ethical decisions. The framework of constrained choice has been applied in the context of farmer decisions about adopting practices that affect a range of issues relevant to the public good, including climate change (Stuart and Schewe 2016), environmental quality, and food safety (Stuart 2009; Baur 2020).

Although constrained choice originally focused on the role of market structure (i.e. the number of firms selling inputs and buying outputs), subsequent scholarship has expanded the concept to identify additional types of constraints that farmers might face. In particular, Baur (2020) draws upon theory from organizational studies to classify constraints into three institutional categories: regulatory ("have to" institutions such as laws and policies), normative ("ought to" institutions such as social conventions), and cultural-cognitive ("want to" institutions such as personal values; Palthe 2014). These are not mutually exclusive, and particular institutional configurations (what Baur calls "carriers") may span multiple categories, as well as organizational levels, from individuals to societies. In the following sections, I provide an overview of four supra-individual carriers that are salient to farmer decision making about insect and landscape management: social networks and conventions, market forces and industry structure, science and technology, and political-legal systems and ideology. I then use them to analyze interviews with Wisconsin farmers that participate—to varying degrees—in the livestock-feed complex which dominates production landscapes in the Midwestern United States.

Institutional carriers of constraint

Social networks and conventions

As much as agriculture is concerned with the biophysical elements of growing plants and animals, it is fundamentally a human activity predicated upon socio-ecological interactions. What and how farmers farm is intimately bound up with their self-identity, as well as the collective identity of the communities in which they are embedded (Bell 2004; Leitschuh et al. 2022). These social conditions influence what practices and behaviors farmers deem possible and in which they are willing to partake. Social networks include family members, farming and non-farming neighbors, university extension agents, crop consultants, and other community members whose opinion farmers may value. When particular production syndromes are normalized in a community, it may be more challenging for an individual farmer to try something new even if they are personally motivated to do so (Ramirez 2013; Wood et al. 2014; Skaalsveen et al. 2020).

Conversely, research has also demonstrated how social networks can be leveraged to catalyze agroecological change (Bell 2004; Warner 2007). In the context of pest management, Warner (2006, 2008) describes social learning partnerships as an alternative to traditional extension models that presume a hierarchical social relations between scientists and growers. Participating California fruit and nut farmers were able to substantially reduce insecticide applications by adopting ecological practices, a feat made possible only by the formation of meaningful social bonds between growers and researchers.

Market forces and industry structure

The ways in which economic systems shape the structure and dynamics of farming is the central concern of agrarian political economy, which developed from rural sociology beginning in the 1960s. Work in this field frequently takes the form of marxist analysis of capitalist agriculture, including how power is concentrated and wielded in agricultural markets (Friedland et al. 1991; Buttel 2001; Bernstein 2016). This scholarship draws attention to both the social and ecological transformations that farm capitalization produces (Weis 2010), frequently framed in the context of Marx's "metabolic rift" (Foster 1999; Schneider and McMichael 2010).

The application of political economy frameworks to environmental issues often falls under the umbrella of "political ecology." Encompassing diversity of scholarly approaches and intellectual traditions, political ecology generally interrogates how power shapes environmental access, management, and change (Goldman and Turner 2011; Robbins 2011). Critical analysis of the pesticide industry, particularly in the Global South, has been a key entomological project for political ecologists (Thrupp 1988; Galt 2008, 2014). Other scholars have turned their attention to the political economy of pesticide use in the Global North, providing historical and structural explanations for why they became the dominant pest management technique in the United States during the 20th century (MacIntyre 1987; Russell 2001). These scholars argue that simplistic explanations like greed and conspiracy on the part of agrochemical companies, while in some cases apparent, fail to capture the interacting biological, economic, and cultural conditions that made chemical pesticides appealing. These include the pesticide treadmill, the risky and competitive nature of U.S. agricultural markets, consumer preferences for unblemished food products, and high-knowledge barriers to alternative management strategies with large uncertainty of effectiveness and low potential for commercialization, among other factors. While many of these conditions persist today, increased salience of negative externalities (i.e. biodiversity crisis, accelerating resistance to insecticide, rising costs for developing new modes of action), new technologies like genetically engineered crops, and advances in ecological pest management science (e.g. landscape perspectives) merit updated analysis.

Science and technology

The status of scientific knowledge about agricultural production and the availability of technologies derived from this knowledge both create and constrain the possible management tools available to farmers. At a basic level, farmers can only act on science that has been done, and can only adopt technologies that exist. Yet, these conditions are not neutral; what remains "undone science" (Hess 2016) and which technologies get developed and deployed are subject to their own social and political constraints (Frickel and Arancibia 2021). The field of science and technology studies (STS) seeks to draw attention to the constructed, contextual nature of scientific knowledge, how scientific claims get deployed and circulated by diverse actors, and (sometimes) how they are used for political ends (Jasanoff et al. 2001; Goldman and Turner 2011).

In a detailed study of entomologists and ecologists in the United States and Canada, historian Paolo Palladino (1996) traced the scientific debates and socio-political conditions that shaped the development of conflicting pest management paradigms over the course of the twentieth century. He argues:

> "Entomologists, even the most ecologically sophisticated ones, were…active participants in the evolution of the insecticide crisis. Not only did they exploit existing institutional formations to advance their goals, they also helped to shape them in ways that both created and foreclosed professional opportunities for their successors to pursue possible alternative relationships between entomology and ecology" (Palladino 1996).

This history illustrates how personal relationships, the organization of research institutions, government funding priorities, and ideology co-produce scientific knowledge about insects and resultant pest control technologies (Jasanoff 2004)

More recent research has turned its attention to the knowledge politics of pesticides, habitat management, and their environmental consequences in the context of pollinator declines (Kleinman and Suryanarayanan 2013; Suryanarayanan and Kleinman 2016; Durant 2019). In particular, they show how diverging standards of evidence and methodological choices by different stakeholder groups (e.g. beekeepers, farmers, academic entomologists, agrochemical companies, and government regulators) produce uneven patterns of ignorance about the causes of pollinator declines as well as feasible solutions. Similar dynamics are likely at play with regards to pests and their natural enemies.

Political-legal systems and ideology

Government policy and regulation has a major influence on the structure of agricultural landscapes and the management practices adopted by farmers (Osteen and Fernandez-Cornejo 2013; Haan et al. 2021). For example, crop insurance subsidies influence farmers' risk calculus and, accordingly, what they grow and how they manage it (Müller et al. 2017; Yu and Sumner 2018). Policies that incentivize the production of particular goods, such as the U.S. Renewable Fuel Standards, can send market signals that narrow the diversity of crops that farmers choose to grow and encourage cropland expansion into previously unfarmed areas (Lark et al. 2022), with negative consequences for biodiversity (Lark et al. 2020). Alternatively, policies may incidentally promote or be intentionally designed for landscape complexity (Landis 2017), such as agri-environmental schemes in the European Union (Hasler et al. 2022).

The legal frameworks and political philosophies underlying specific policies may also manifest on the landscape. In her comparative study of three townships in Wisconsin's Kickapoo valley, Lynn Heasley demonstrates how the contrasting approaches to property rights among of settler communities, Amish farmers, and ancestral Ho-Chunk land stewards created markedly different arrangements of farm fields, forests, and grasslands over space and time (Heasley 2012). Various other theoretical and empirical treatments show similar dependence between property relations and land use patterns (particularly in agriculture), leading some scholars to argue that private land property regimes are fundamentally at odds with agroecological production systems (Calo et al. 2021).

Pervasive ideological forces deeply embedded in culture often underlie and interact with all of the aforementioned institutional constraints on farmer management decisions. In the United States, individualistic ideals have particular hold on the national rural imagination. The trope of the self-sufficient "Yeoman farmer" (Calo 2020) and associated settler-colonial culture of rugged individualism on the American frontier (Bazzi et al. 2020) are important socio-cultural myths that structure beliefs about what a "good farmer" is and does. A more recent manifestation of this individualistic ethos comes in the form of neoliberalism, an economic philosophy and policy package associated with trade liberalization, deregulation, privatization, and general withdrawal of the state from public life in favor of free enterprise (Harvey 2007), with important consequences for agriculture and the environment (Igoe and Brockington 2007; Castree 2008; Busch 2010). Neoliberal ideology can also remake shared notions of citizenship, feeding back to influence individual farmer values and behaviors (Haggerty et al. 2009; Stock et al. 2014)

Case study: insect and landscape management in Wisconsin

Given this suite of possible institutional constraints on farmer management, I sought to understand the extent to which different types of constraints—social, economic, scientific, and political—matter for insect pest control, biodiversity conservation, and landscape structure. To do this, I conducted semi-structured interviews with ten commercial farmers in Southern Wisconsin in the summer of 2021. While a case study of this size cannot offer quantitative claims about the general attitudes and practices of all Wisconsin farmers, it is sufficient to identify central themes and derive meaningful theoretical insights (Guest et al. 2006). I begin this section by providing a brief overview of the agricultural industry in the study region, followed by a description of research methods and analysis, and conclude with presentation and discussion of key findings.

Agriculture in Wisconsin

Agriculture is one of the largest industries in the state of Wisconsin (about 16% of the state's economy; Deller 2019), and Wisconsin is in the top ten agricultural producing states in the country. The sector is dominated by dairy farming, which functions as part of what some scholars have termed the grain-oilseed-livestock complex (Friedmann 1991; Weis 2013). Unlike neighboring corn belt states, Wisconsin still retains a significant amount of livestock integration with cropping systems, though the structure of the industry has changed dramatically over the past half century. In particular, the state has seen a precipitous decline in the number of operating dairies (down from over 100,000 throughout the first half of the twentieth century to less than 7,000 today) and simultaneous increases in average farm size and milk production (MacDonald et al. 2020).

These conditions have created a patchy agricultural landscape that includes large commodity grain monocultures of corn and soybean, alfalfa, and mixed hay supporting a confined animal feeding model of dairy and beef operations. A smaller proportion of land is devoted to small grain (wheat, oats, rye) production or pasture-based livestock grazing systems. The grain-oilseed-livestock complex covers approximately 90% of Wisconsin farmland (USDA NASS 2022). Some parts of the state also have large ares of specialty crop production including potatoes and cranberries, though these industries and growing regions are beyond the scope of the present study.

Participants, interviews, and analysis methods

Farmers were recruited from a contemporaneous ecological study investigating the effects of spatio-temporal landscape patterns on aphids and their lady beetle predators in Southern Wisconsin, USA (Chapter 1). Participants were not selected to be a representative random sample of all Wisconsin farmers, but rather a targeted theoretical sample (Glaser and Strauss 1967; Orne and Bell 2015) spanning a gradient of production systems and landscape context. All farmers produced some combination of commodity grains, livestock forage (including pasture), dairy, and meat (typically beef). All participants were white men above the age of 35, consistent with demographic patterns of land-owning producers in the state (99% white, 65% male, 90% over 35; USDA NASS 2017). They ranged from grain farmers growing just two crops (corn and soybean) with no livestock, to dairy farmers growing multiple grain and forage species as livestock feed, to a beef farmer rotationally grazing cattle on diverse perennial pasture. Farms also spanned a gradient of landscape context, ranging from over 90% cropland within 2 km around their farms to just 10% (with the remaining land area dominated by natural and semi-natural habitats such as prairies, wetlands, and forest).

All interviews were conducted on-farm between July and September 2021. Interviews were based on a guide (Supplement 1) developed to elicit responses related to four overarching questions:

1. What insects do farmers identify as relevant to their production, and what are their attitudes toward insects on the farm in general?
2. Do farmers perceive "the landscape" around their farm as a resource or liability?
3. How, if at all, do farmers respond to practices on neighboring farms when making pest control decisions?
4. What environmental, social, regulatory, and/or economic conditions influence farmers to engage in particular insect and landscape management practices?

Interviews lasted between 30 and 90 minutes. Transcriptions of interviews were coded using NVivo (QSR International Pty Ltd. 2019, https://lumivero.com/products/nvivo/). I employed an initially deductive but iterative coding approach, beginning with an initial set of hierarchical thematic codes which were subsequently revised and updated as new themes emerged (Fereday and Muir-Cochrane 2006; Orne and Bell 2015). Initial themes included farm production factors, insect taxa, pest management practices, landscape thinking, and the institutional carriers described above. Themes added after initial transcript review included multifunctionality, profitability, and soil health (see Supplement 2 for a complete coding tree). In the analysis below, I narratively synthesize these themes and illustrate them with interview quotes lightly edited for length and clarity.

Results and discussion

PEST-CENTRIC NARRATIVES AND MANAGEMENT CONSTRAINTS

Farmers' knowledge of insects was variable, and did not neatly align with farm type or landscape context. In general, farmers had greater knowledge of pest than beneficial species. Across all interviews, they identified 10 pest taxa as being present in their fields, the most common of which were Japanese beetles (*Popillia japonica* Newman; six farmers), corn rootworm (*Diabrotica virgifera* LeConte; five farmers), aphids (family Aphididae; four farmers) alfalfa weevil (*Hypera postica* Gyllenhal; three farmers) and potato leafhopper (*Empoasca fabae* Harris; three farmers). In contrast, most farmers did not name specific beneficial insect taxa they knew to be in their fields, even if they were familiar with the concept of pollinators and natural enemies in general. An exception was one commodity grain farmer in a crop-dominated landscape who had a personal interest in insects and named over a dozen beneficial or non-pest arthropod taxa over the course of the interview, including bumble bees, spiders, crane flies, paper wasps, dragonflies, lacewings, and lady beetles; however, when asked, he indicated that he did not consider these organisms when making pest management decisions.

Another notable exception to the general lack of discussion of beneficial insect species was the monarch butterfly (*Danaus plexippus* L.), which was mentioned by three farmers, though not all saw clear utility to its conservation. As one dairy-beef farmer noted, "With the monarch butterfly…if there's milkweed out there you try to leave that alone. You know, I don't know what they do, but you try to leave it alone." Another dairy farmer expressed interest in the monarch because of a government program that would pay him to plant milkweed on unfarmed land. Amused, he remarked: "You know, we try to kill milkweed in the corn ground, but now we're going to plant it here!" This observation is emblematic of a process that is well-documented by political ecologists studying neoliberal conservation, namely the deregulation and subsequent re-regulation and commodification of nature (Robertson 2006; Igoe and Brockington 2007; Castree 2008). As insect ecologists have argued, changing weed management regimes associated with the shift to genetically engineered herbicide-tolerant crops have contributed to monarch habitat loss and population declines (Pleasants and Oberhauser 2013; Haan and Landis 2019). Rather than regulate such biodiversity-degrading practices, the government program described by the farmer is an example of a payment for ecosystem services (PES) scheme that seeks to incorporate public goods into private market logics via incentives to individual landowners . This example represents an ecological management constraint placed on farmers by one institutional carrier (a consolidated seed and chemical industry) and attempted alleviation by another (government conservation policy), all operating within the ideological constraints of neoliberalism.

Farmers identified four practices they employed to manage insect pests in their fields: crop rotation, insecticides, surveillance of pest populations, and genetically engineered Bt-crops. All of these are elements of the traditional IPM paradigm. No farmers identified landscape-scale management practices for pest control, though some discussed such practices in a different context (see below). All farmers growing crops identified rotation and pesticides as key tools in their pest management toolkit. Crop rotation is a centuries-old practice that remains an important strategy for interrupting pest and disease cycles. Most farmers spoke to the value of keeping at least a two-crop rotation, though some also acknowledged that this wasn't always possible given their livestock feed requirements. Commodity markets also incentivize farmers to grow whatever fetches the best price, and punishes them for keeping rotations that could be beneficial for agroecological reasons:

> "I've found that we do a really good job growing corn, that is our most profitable crop. I was talking to this guy, he says, "Maybe you need to take a hit on your wheat just for the rotation." And it's like, "Yeah, I know, that's a management tool. But the thing is…you can make a lot more money" (Corn and soybean farmer).

Furthermore, some farmers noted that consolidation in the market for farm outputs had constrained their ability to rotate crops:

> "I do like a little more diversity. We used to have a lot of canning crops. We would have 300 acres of peas, 300 acres of sweet corn, 50 to 70 acres of green beans….We really don't have a whole lot of opportunity to grow them. We used to grow for Del Monte, which was out of Arlington, there was a canning factory there. And the whole area here grew peas and sweet corn [for them]. Well, back in the late 80s/early 90s, they made a decision that they were going to close that plant. The only other option would have been Lodi Canning, and you have to grow peas in order to get sweet corn [contracts], and with our no-till we just don't care to have the peas, because they're going to come in and harvest them and…leaving ruts in your ground" (Corn and soybean farmer).

These examples illustrate structural market forces interfering with a farmers' ability to maintain multiple ecological management practices (in this case, diverse crop rotations and reduced tillage), a classic example of market-based constrained choice (Hendrickson and James 2005). Other farmers pointed to federal policies that hindered diversification: "If you pulled the [commodity grain] subsidy program, the land diversification I think would change immensely....And I think it would probably put some livestock back in a fair number of operations." Despite such barriers, some farmers were actively trying to diversify and lengthen their rotations, though not always for pest management reasons (see below).

The circumstances under which farmers decided to spray insecticides varied widely. Some used neonicotinoid seed treatments and prophylactic sprays, while others would scout for pests and spray only when they reached economic thresholds. Farmers' tolerance for pests also varied depending on what the end-use of their crop would be. In particular, crops grown for livestock tend to have more relaxed quality standards, requiring fewer (and in some cases no) insecticides. This was noted by a large-scale dairy farmer growing small grain for feed ("Wheat, we don't spray for nothing, you know, unless something would come in there really bad") and a small-scale beef farmer rotationally grazing cattle ("In the pastures, you know, we don't spray, we don't use any harmful chemicals"). Another dairy farmer pointed out that the interaction of multiple agro-industrial trends such as growing field sizes, high commodity prices, and available technologies were changing patterns of pesticide application across the landscape:

> "One thing really catching on around here is spraying with planes. Down in Central Illinois it's a very common practice, and it's working this way. Some people are just automatically spraying. They have it all calculated: the cost of the plane, the spraying, down to so many bushels per acre. And with $6 corn, you know, it didn't take near as many bushels to justify this. When you're in the marketing end, you can sell that crop right to the elevator, and you get a check back. Well we take a lot of that corn and we put it through the cows, and we do not see a return on our corn until the cows produce milk and cheese. You have to kinda figure out where you made your money" (Dairy farmer).

Crop-livestock integration thus has the potential to maintain refugia for insects on the landscape, and may also serve as a reservoir for natural enemies that are drawn to areas of high prey density (Pons et al. 2005; Chapter 3). On the other hand, industry trends toward consolidation and disarticulation of crop and livestock production (a “metabolic rift”) may create market pressures that increase pesticide use.

Some farmers indicated that they would prefer to dispense with pesticides altogether, but that this wasn’t possible given perceived market constraints: “I’d quit using chemicals tomorrow if I could, but just isn't economically feasible. I think if I tried to go organic I'd be out of business in two years. I'm sorry, that's just how it is.” New technologies like crops genetically engineered to produce *Bacillus thuringiensis* toxin (Bt) are intended to reduce the need for insecticide sprays, but farmers had a wide variety of opinions about this technology and its shortcomings. Some had happily adopted so-called “quad-” or “triple-stacked” corn varieties engineered to be toxic to beetle and caterpillar pests as well as resistant to glyphosate and glufosinate-ammonium herbicides: “It's got all the traits in it. It costs a little more, but you're secure and like an insurance policy. Or you can go with a cheaper brand, and then the bugs do get in and you didn't gain nothing anyways.” Another farmer stated that he used Bt corn because it was preferable to insecticides, but would prefer not to if he could avoid it with a longer crop rotation. Yet another farmer was skeptical of the value of Bt corn, observing:

> “A fair number of people buying rootworm-traited corn seem to be having enough pressure from rootworms anyhow, that they still either end up with damage and yield losses, or they're putting insecticide on anyway. So I've stayed away from the rootworm-traited stuff and just bought the insecticide” (Dairy farmer).

Finally, one farmer who planted genetically engineered corn told me he did so “not necessarily for the Bt”:

> “The [yield potential] genetics are there and when they include the Bt, it's like, they really encourage you with the pricing that they have for it. If it's gonna cost me five dollars more, I'll take that, you know, versus nothing.” (Corn and soybean farmer).

This last point suggests one reason why Bt corn was so rapidly and widely adopted across the United States, now covering 84% of planted acres (USDA ERS 2022), which contributed to area-wide suppression of pests, but also high rates of Bt resistance in the United States (Tabashnik et al. 2023). The evolution of resistant pests is another example of a landscape-scale collective action problem created in part by constrained choice, since farmers have high incentive to adopt uniform pest control technologies across large spatial extents, but little incentive to contribute to resistance monitoring and reporting (Andow et al. 2017).

LANDSCAPE THINKING, OR LACK THEREOF

The practices farmers identified for controlling pests largely ignored potential contributions of predatory insects and biological control, and were restricted to field-scale interventions. When asked about how off-crop habitat (such as nearby woodlots or grasslands) might affect insect populations in their fields, most had little to say; statements like “I wouldn't know anything about that,” and “I never thought they did anything bad or good” were common. Some farmers indicated that it was plausible that these habits could be sources of pests, but that they had not observed any effects on their farm:

> "I do know root worms will migrate onto pastured ground or fallow ground. But you know, I don't know if it would ever be to the degree sure that it would affect your regular farming operation" (Dairy farmer).

> "I guess I don't worry about it from an insect standpoint. Maybe if there was a larger amount of wooded area around me, it would be a larger concern. But at this point, I don't see it being too much of a factor" (Dairy farmer).

Several farmers noted the value of woodlots for income stream diversification and multifunctionality (Van Huylenbroeck et al. 2007, Renting et al. 2009). Identified use values of woodlots included timber harvest (three farmers) and hunting (three farmers). Interestingly, the habitat that wooded areas provided to vertebrate wildlife also posed a minor pest management challenge for some farmers, who identified deer and racoons grazing at field edges as occasional "four-legged pests." Along these lines, configurational dimensions of landscape structure (e.g. field size, edges with non-cropland) seemed to be of greater concern to farmers than compositional ones. Several noted that crop fields bordering woodlands tended to suffer yield losses due to shading, and that smaller fields were inefficient for operating large farm equipment:

> "We've eliminated fence lines here. Not only is it unproductive, because, if you've got a fence down in the middle of this field, you just double the times you have to turn around—whether it's the planner, the sprayer, whatever, that causes inconsistencies in the field and yield loss....So you eliminate that issue, you've you've solved a lot of a lot of problems" (Corn and soybean farmer).

Other farmers, especially those still operating at small-scales with older equipment, were more skeptical that bigger fields were always better for their production system and geographic context. As one dairy farmer described:

> “I know everybody likes to get bigger fields. But it's a little harder to control the water and the contours and things like that, in my opinion. I understand the bigger field thing, but I also like to keep my soil in place. I do wonder, many times when I see a 160 acre field, with soybeans going every which direction on the slopes of the land, you know, how much soil do they lose? You can't hardly plant all the little nooks and crannies against the slope of the land as well in the larger fields” (Dairy farmer).

Another dairy farmer described that the shift away from dairies to cash cropping and new planting, spraying and harvesting technologies were major drivers expanding field sizes, eliminating tree cover, and dwindling crop diversity across the landscape:

> Today with the cash crops moving into the area, the fence lines that are getting torn out are phenomenal…We have neighbors around us that are basically farming from road to road today. It used to be our contour strips were 7 feet wide. Now they’re 96 feet, we tried to match up to our corn planter….All the equipment is getting bigger and these guys are spending like a half a million dollars on a combine. They don't want to smash their half-million dollar combine on a tree limb, and you can’t blame them….Today a big cash cropper will come in and he'll put the whole farm in corn. And then the following year, that whole farm goes into beans (Dairy farmer).

While the importance of crop diversity in time (i.e., rotation) was obvious to all farmers, perceptions about the value diversity across space were less clear. Some acknowledged that having multiple crop types around might prevent the build up of pests of any particular crop to extreme levels. However, they did not articulate potential effects on natural enemies, and this pest-centric lens meant they tended to perceive the insect communities on different crops as largely distinct:

> “It isn't like the hay field has weevils in it, and jumps on the corn. You know, or vice versa. If the corn has a root worm in it or something. It isn't like it's gonna go get on the alfalfa” (Dairy farmer).

An additional component of landscape thinking involved the extent to which farmers responded to or coordinated with their neighbors when making management decisions. Participants varied in their recognition of neighboring farmers’ influence on their own practices. Some said they paid no attention (“I don't care at all what they're doing”; “We don't talk about yield. We don't talk about anything”), while others argued that all farmers are paying attention to each other, even if they don’t acknowledge it (“In farming, you’re all the Joneses!”). Several farmers stated that observing others—their successes and mistakes—was an important source of knowledge about good farming:

> “If you want to learn how to farm your farm, watch your neighbors. Don't don't do anything wild. Do what they're doing. Learn from your neighbors. It's very important around here” (Dairy farmer).

Finally, two farmers using “alternative” agricultural practices (highly diverse rotations, polycultures, livestock integration, and/or rotational grazing) expressed worries about the negative effects their conventional farming neighbors could have on their own farm and the environment:

> “One of the concerns about what the neighbors [are doing] is if they're managing a non-diverse rotation, and end up creating some weeds or insects that are very adapted against all the management practices that we have available right now from herbicides to insecticides. If a population adapts to basically everything that we've got and it moves across the fenceline, how am I going to manage it? I feel that leaves a lot of opportunity for pest populations to adapt and become quite successful, without any diversification and nothing to mix things up.” (Dairy farmer).

> “From what I've observed, [the neighboring farm’s] fields are just totally sterilized for the year and there's no life. Our side of the road will be alive with frogs, and the other side will just be silent. So I'm sure that affects our ecosystem in a way—maybe there's less stuff here, because they can't get here, traverse into our farm. It seems like an oasis” (Rotational grazier).

As these examples illustrate, farmers are aware of the ways agriculture and biodiversity can be affected by landscape processes (i.e., those occurring at scales larger than individual fields). However, most did not think of them explicitly as such, and did not consciously incorporate landscape considerations into management decisions. Some farmers did mention participation in local watershed groups, which can serve as a forum for landscape-scale coordination and planning (Floress et al. 2009, Hall 2016), but did not describe these activities in relation to insect or biodiversity outcomes. This is representative of the broader environmental priorities of interview participants.

CONTRASTING CONSERVATIONS, SCALAR MISMATCH, AND PROBLEM CLOSURE

The environmental impacts of agriculture are not absent from farmers’ sphere of concern. Environmental “conservation” in particular is common parlance (as in “conservation agriculture”; Hobbs et al. 2007), though the term tends to take on a different connotation in the farm sector compared to its use by the environmental movement or research scientists. Among these latter constituencies, “conservation” is closely associated with biodiversity and protection of habitat for wildlife (as in the discipline of of “conservation biology”). In contrast to this primarily biotic understanding, when farmers in the U.S. talk about “conservation” they are primarily referring to practices that prevent soil erosion and water loss, a decidedly more abiotic definition. The reason for this discrepancy likely finds its legacy in the USDA Soil Conservation Service, an agency founded in the 1930s in response to the recognition that "the wastage of soil and moisture resources on farm, grazing, and forest lands…is a menace to the national welfare." The agency changed its name to the Natural Resources Conservation Service in the 1990s "to better reflect the broadened scope of the agency's concerns" (NRCS n.d.), but the strong association among farmers of "conservation" with soil persits and extends beyond the context of the agency.

These abiotic conservation priorities were evident among farmer participants with a variety of production systems when discussing their motivations for adopting ecological management practices. One corn and soybean farmer who had started no-till management in his fields over two decades ago cited soil improvement as a major catalyst. A dairy farmer that had begun planting rye for livestock feed similarly remarked that he maintained this practice because it had "turned into being a good way to conserve soil" and "proven to help erosion tremendously." The rotational grazier cited "an environmental motivation to stop the erosion of topsoil by putting down perennials" when he made the decision to convert his family farm from feedlot- to grass-finished beef.

Soil was also a top priority for the participant with the most diversified operation in my sample, a small-scale dairy farmer raising cows on a combination of pasture, species-rich hay mixtures, and six crops grown in various combinations as contour strips, cover crops, and intercrops:

> "My long term thought is that the driving factor, the biggest value on the farm, is the soil. And that diversification, that long term-thought process, should build soil and keep soil in place. At the end of the day, that's what's gonna drive your long-term productive capacity, whatever crop it is you're growing. And so that's kind of my driving factor of why I'm doing it" (Dairy farmer).

While the widespread farmer appreciation for soil conservation over biodiversity (and in particular, beneficial insect) conservation may have both agronomic and historical basis, its contemporary manifestations may have additional ecological and political-economic dimensions. Specifically, "soil conservation"—and increasingly "soil health" (Lehmann et al. 2020)—are agro-environmental concepts well-suited to neoliberal conservation and private land ownership, because of the individual scale at which management interventions occur and the accrual of benefits to private landowners. In contrast, many ecological processes influencing "conservation biological control" and related approaches to pest management occur at landscape scales, necessitating collective management interventions in the service of the public good. This poses a fundamental constraint to widespread acceptance and adoption.

At a purely biophysical level, soil is (mostly) stationary, while insects are mobile and transcend field and farm boundaries. When soil moves around (i.e. erosion and runoff), it is indicative of poor management—well-managed soil should remain within the property lines of individual private landowners, who are the preferred targets of neoliberal conservation schemes like PES (Fletcher and Büscher 2017). Insects, on the other hand, cannot really "belong" to any individual farmer. There is thus a "scalar mismatch" between the biology of many organisms involved in agricultural production outcomes (pests, natural enemies, pollinators) and the management options that are on the neoliberal table. Liboiron (2021) defines scalar mismatch as a situation in which “problems and their proposed solutions occur at different scales and do not affect the relationships that matter.” While-field level practices can matter, they are insufficient for the effective conservation of insect biodiversity and associated contributions to human wellbeing (Haan et al. 2021, Tscharntke et al. 2021). The ideological nature of neoliberalism means that it not only creates structural barriers to landscape-scale insect management, it also narrows the scope of what farmers and scientists deem possible, reframing the problem of pest control in terms of socially and politically acceptable solutions, setting the agenda for subsequent study, and constraining alternative paradigms. This is process is known as “problem closure” in the STS literature (Hajer 1995, Guthman 2011)

Evidence of neoliberal problem closure was apparent in the responses of farmer participants. Even for those farmers who were personally motivated to change their production systems to practice more ecologically-sound agriculture, the path to landscape scale change was decidedly individualistic and market-oriented. In response to a question about the possibility of crop subsidy reform to diversify and perennialize agriculture, the rotational grazier remarked:

> “That would be fantastic. But there's too strong of a lobby, right? Not gonna happen. That's why I have more hope in the private sector, that if there's money to be made by big companies, and they get together as best they can, they can go ahead and do it. I’m more optimistic about that” (Rotational grazier).

Conclusion

Crop production systems will likely require large-scale redesign to provide for human societies while halting degradation of the other species on which they depend (Foley et al. 2011, Perfecto et al. 2019, Kleijn et al. 2019, Haan et al. 2021). Despite advances in ecological science demonstrating the importance of landscape-scale processes in promoting pest suppression and the conservation of beneficial insects, habitat management coordination among farmers remains sparse and landscape simplification proceeds largely unabated. In this study, I used a framework of constrained choice to argue that overlapping structural, socio-economic, and political factors contribute to the present state of affairs. By interviewing farmers with diverse production systems and values across a range of landscape types, I demonstrated that they are largely subject to the same constraining forces that act to co-produce simplified agricultural landscapes, despite the best efforts of some farmers to chart alternative futures.

Popular narratives about insect declines are typically framed at world-ending scales. descriptors like “apocalypse” (Jarvis 2018) “armageddon” (Carrington 2017; Kover 2019), and “the collapse of nature” (Carrington 2019) have all figured prominently in media representations of the emerging ecological crisis. Yet such environmental apocalypticism has been convincingly critiqued for its depoliticizing tendencies. Writing on climate change, geographer Erik Swyngedouw has argued that apocalyptic imaginaries have been a central mechanism by which the public sphere has been made “post-political” (Swyngedouw 2010, 2013) By appealing to a universal and totalizing threat of rising CO_2, apocalypticism breeds complacent populism, obscures power differentials and forecloses proper functioning of politics as the clash of "competing visions of a different socio-ecological order" (Swyngedouw 2010). Government is relegated to a managerial role, only permitting interventions that shore up capitalist production in the face of impending doom, ignoring the apocalypse that is already here for many—including non-human beings (Collard 2013).

The insect apocalypse narrative shares many of the same features as the climate apocalypse narrative, especially its depoliticizing universalism. The constraints to more abundant insect futures (Collard et al. 2015) that I have outlined should not contribute to complacency, but rather illuminate where concerned publics should target their efforts to effect change. Farms are not islands. They are embedded in a biophysical and political-economic landscape that simultaneously affect and are affected by their functions. While this collective interdependence may be inconvenient for a political-economic system that favors atomization and the commodification of food and nature in liberal markets, recognizing and leveraging it will be a necessary condition for the mutual flourishing of humans and the rest of nature.

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Appendix 4.1 – Interview Guide

Demographic information

- Tell me about yourself and how you started farming.
- What do you grow/produce on your farm?
- How, if at all, has this changed over time?
- How do you decide what to grow?

Insect perceptions

- What insects are on your farm?
- Pests vs. beneficials?
- How do you manage them?
- Where do you get your pest management information from?

Landscape thinking

- How, if at all, do you think different fields affect each other?
- Does the unfarmed land on your property affect your operation? How?
- Are some parts of your farm more or less prone to insect outbreaks?
- Do you consider what or how your neighbors are farming when making management decisions?

Wrap up

- Is there anything else you wanted to share that I didn't ask about?
- Do you have any questions for me?

Appendix 4.2 – Coding Tree

- Insects
    - Beneficials
    - Pests
- Pest management
    - Rotation
    - Pesticides
    - Surveillance
    - Genetically engineered crops
    - Habitat management
- Landscape
    - Composition
    - Configuration
- Farm outputs
    - Grains
    - Feed
    - Dairy
    - Beef
- Constraints
    - Individual
    - Social
    - Industry & Markets
    - Science & Technology
    - Policy
    - Ideology
- Multifunctionality
- Profitability
- Soil Health