

From landscape patterns to behavioral processes: land cover and climate effects on insects in
agricultural systems

by

Nicole Beth Kucherov

B.A., Roger Williams University, 2010
M.A., Miami University, 2018

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Entomology
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2026

Abstract

Agricultural insect pests are influenced by factors ranging from landscape composition to plant chemical cues, yet we often manage them on a field scale. Although our concerns are often focused on pest insect abundances within one field, insect populations are interacting with the landscape and other insect populations across multiple scales during their dispersal, across life stages, and through trophic interactions. As society moves towards more sustainable agroecosystems and precision agriculture, it is important to consider insect ecology and implement a multi-scale approach for pest management. Consistent landscape effects on insect populations are difficult to identify due to large variations in crop type, natural habitat type and field configuration, as well as spatial and temporal variations in climate across studies. This dissertation investigates how surrounding landscape composition and climate shape insect communities within agriculture fields across strong landcover and precipitation gradients but within one consistent crop type while also considering the effects of bordering fields. Then, on a broader scale, how regional land cover and climate influence the spread of the invasive agricultural pest *Popillia japonica* Newman over time. And lastly, at a finer scale investigates a semiochemical-based mechanism for the behavioral response of *P. japonica* to intercropping. Together, these studies form a multi-scale viewpoint that considers multiple habitat associations across different life stages, dispersal, and chemosensory-based foraging.

First, in a field study, we evaluated effects of landscape composition, precipitation, and bordering edge on insect abundance and community composition within soybean fields along a semi-natural gradient. We found that surrounding semi-natural areas affected the insect community, increasing pollinator abundance and decreasing pest abundance. We found evidence of significant interactions, where precipitation can minimize land cover's effects on beneficial

insect populations at lower levels. The interaction between land cover and precipitation suggests that low precipitation results in physiological constraints to the natural plant populations that have an indirect impact on beneficial insects through land cover in addition to the direct effect of low precipitation on the insects themselves.

Second, in a regional study of the spread of the invasive Japanese beetle, *Popillia japonica* at the leading edge of an invasion front in the central United States, we identified habitat associations and predicted future spread, producing county scale risk maps for use in monitoring and risk assessment. Beetle occurrences were positively correlated with developed areas, corn and soybean, minimum temperature, and precipitation, and negatively correlated with grassland and pasture, and maximum temperature. There was high probability of occurrence for Japanese beetles across the entire region. Here we see the importance of habitat across various life stages as developed areas are necessary for providing *P. japonica* larvae with turf grass and adults can feed on corn and soybean. We also see the importance of climatic variables of temperature and precipitation which exert physiological constraints on the development and survival of *P. japonica*. Interestingly, we found a negative correlation with grassland and pasture despite grass roots being the preferred food source for larval *P. japonica*. This is likely due to regional differences in grassland root systems and a trophic interaction with grassland birds, who are natural predators of *P. japonica*.

Third, we investigated a semiochemical-based mechanism for the behavioral response of *P. japonica* to intercropping soybean with sorghum. Although we found unique semiochemical profiles among our treatments, *P. japonica* did not show a significant preference for our treatment extracts over controls or to any of the treatments in a dual choice assay. If intercropping soybean with sorghum significantly affects the behavior of *P. japonica* in the field,

it is likely to occur at a different scale, or in response to non-olfactory stimuli. The lack of a behavioral response to semiochemical differences in isolation, despite earlier field studies suggesting this as the mechanism for their observed differences in abundance at the field-level, indicates that *P. japonica* are making decisions across multiple senses and scales.

Our results indicate that insect communities in agricultural fields are shaped by interacting effects of landscape composition and climate, but also that the strength and direction of these effects depend on processes operating at multiple, nested scales. Our field-scale findings demonstrate that semi-natural habitat can reduce the abundance of key soybean pests, including the Japanese beetle. Yet the observed interaction between precipitation and land cover suggests that the positive effect of natural land on the beneficial ecosystem services by natural predators and pollinators may be diminished under low precipitation conditions.

Similarly, we see that on a regional-scale, temperature and precipitation are important factors in moderating the distribution and spread of *P. japonica* across the landscape. These regional patterns constrain expectations of *P. japonica* infestation at the field scale, as local management decisions are nested within regional landscape composition and climatic suitability. At the behavioral scale, the lack of response to semiochemical cues on a local scale suggests that mechanisms often assumed to drive plant-insect interaction patterns may not operate as expected in the absence of other cues. In this case, *P. japonica* responses to intercropping soybean and sorghum likely emerge from multi-sensory cues or from interactions within landscape context. Together, these findings highlight that field-scale management strategies are limited by regional climatic and landscape context and depend on behavioral mechanisms that may not scale linearly, underscoring the need for integrative, multi-scale approaches to sustainable pest management.

From landscape patterns to behavioral processes: land cover and climate effects on insects in
agricultural systems

by

Nicole Beth Kucherov

B.A., Roger Williams University, 2010

M.A., Miami University, 2018

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

Department of Entomology
College of Agriculture

KANSAS STATE UNIVERSITY

Manhattan, Kansas

2026

Approved by:

Major Professor
Dr. Tania Kim

Copyright

© Nicole Kuchеров 2026.

Abstract

Agricultural insect pests are influenced by factors ranging from landscape composition to plant chemical cues, yet we often manage them on a field scale. Although our concerns are often focused on pest insect abundances within one field, insect populations are interacting with the landscape and other insect populations across multiple scales during their dispersal, across life stages, and through trophic interactions. As society moves towards more sustainable agroecosystems and precision agriculture, it is important to consider insect ecology and implement a multi-scale approach for pest management. Consistent landscape effects on insect populations are difficult to identify due to large variations in crop type, natural habitat type and field configuration, as well as spatial and temporal variations in climate across studies. This dissertation investigates how surrounding landscape composition and climate shape insect communities within agriculture fields across strong landcover and precipitation gradients but within one consistent crop type while also considering the effects of bordering fields. Then, on a broader scale, how regional land cover and climate influence the spread of the invasive agricultural pest *Popillia japonica* Newman. And lastly, at a finer scale investigates a semiochemical-based mechanism for the behavioral response of *P. japonica* to intercropping. Together, these studies form a multi-scale viewpoint that considers multiple habitat associations across different life stages, dispersal, and chemosensory-based foraging.

First, in a field study, we evaluated effects of landscape composition, precipitation, and bordering edge on insect abundance and community composition within soybean fields along a semi-natural gradient. We found that surrounding semi-natural areas affected the insect community, increasing pollinator abundance and decreasing pest abundance. We found evidence of significant interactions, where precipitation can minimize land cover's effects on beneficial

insect populations at lower levels. The interaction between land cover and precipitation suggests that low precipitation results in physiological constraints to the natural plant populations that have an indirect impact on beneficial insects through land cover in addition to the direct effect of low precipitation on the insects themselves.

Second, in a regional study of the spread of the invasive Japanese beetle, *Popillia japonica* at the leading edge of an invasion front in the central United States, we identified habitat associations and predicted future spread, producing county scale risk maps for use in monitoring and risk assessment. Beetle occurrences were positively correlated with developed areas, corn and soybean, minimum temperature, and precipitation, and negatively correlated with grassland and pasture, and maximum temperature. There was high probability of occurrence for Japanese beetles across the entire region. Here we see the importance of habitat across various life stages as developed areas are necessary for providing *P. japonica* larvae with turf grass and adults can feed on the corn and soybean. We also see the importance of climatic variables of temperature and precipitation which are providing physiological constraints on the development and survival of *P. japonica*. Interestingly, we found a negative correlation with grassland and pasture despite grass roots being the preferred food source for larval *P. japonica*. This is likely due to regional differences in grasslands and a trophic interaction with grassland birds, who are natural predators of *P. japonica*.

Third, we investigated a semiochemical-based mechanism for the behavioral response of *P. japonica* to intercropping soybean with sorghum. Although we found unique semiochemical profiles among our treatments, *P. japonica* did not show a significant preference for our treatment extracts over controls or to any of the treatments in a dual choice assay. If intercropping soybean with sorghum significantly affects the behavior of *P. japonica* in the field,

it is likely occurring at a different scale, or in response to non-olfactory stimuli. The lack of a behavioral response to semiochemical differences in isolation, despite earlier field studies suggesting this as the mechanism for their observed differences in abundance at the field-level, indicates that *P. japonica* are making decisions across multiple senses and scales.

Our results indicate that insect communities in agricultural fields are shaped by interacting effects of landscape composition and climate, but also that the strength and direction of these effects depend on processes operating at multiple, nested scales. Our field-scale findings demonstrate that semi-natural habitat can reduce the abundance of key soybean pests, including the Japanese beetle. Yet the observed interaction between precipitation and land cover suggests that the positive effect of natural land on the beneficial ecosystem services by natural predators and pollinators may be diminished under low precipitation conditions.

Similarly, we see that on a regional-scale, temperature and precipitation are important factors in moderating the distribution and spread of *Popillia japonica* across the landscape. These regional patterns constrain expectations of *P. japonica* infestation at the field scale, as local management decisions are nested within regional landscape composition and climatic suitability. At the behavioral scale, the lack of response to semiochemical cues on a local scale suggests that mechanisms often assumed to drive plant-insect interaction patterns may not operate as expected in the absence of other cues. In this case, *P. japonica* responses to intercropping soybean and sorghum likely emerge from multi-sensory cues or from interactions within landscape context. Together, these findings highlight that field-scale management strategies are limited by regional climatic and landscape context and depend on behavioral mechanisms that may not scale linearly, underscoring the need for integrative, multi-scale approaches to sustainable pest management.

Table of Contents

List of Figures	xiii
List of Tables	xvii
Acknowledgements	xviii
Dedication	xxi
Chapter 1 - Introduction.....	1
IPPM: A landscape approach.....	5
Soybean: a dominant land cover in the central U.S. landscape	10
<i>Popillia japonica</i> Newman: a landscape pest	11
References	15
Chapter 2 - Precipitation moderates the effects of surrounding landscape composition on insect communities.....	22
Abstract.....	22
Introduction.....	24
Methods	28
Study Region	28
Site selection	30
Insect community sampling and abundance calculations:	32
Seasonal climate data	33
Landscape analysis.....	34
Statistical analysis	36
Constrained Ordination Analysis	40
Results.....	41
Landcover and climate effects on pest abundance and community composition	42
Landcover and climate effects on predator abundance and community composition	46
Landcover and climate effects on pollinator abundance and community composition	48
Location within field, but not ecoregion, affected insect abundance, while both influenced community composition.....	51
Discussion	53
Surrounding natural land cover and precipitation.....	54

Pest community composition	55
Predator abundance and communities	56
Pollinator abundance and communities	58
Field edges	59
Conclusion	60
References.....	63
Chapter 3 - Climate and human-modified landscapes influence spread of invasive agricultural	
pest <i>Popillia japonica</i> Newman in American Midwest and Great Plains	75
Abstract	76
Introduction.....	76
Methods	81
Study Area	81
Data collection	82
Data conversion	84
Generalized additive models	85
Forecasting data	86
Results.....	87
Model performance and validation	87
Relationships with predictor variables	88
Model predictions	90
Discussion	92
Conclusion	99
References.....	100
Chapter 4 - Investigating a semiochemical-based mechanism for the beneficial activity of	
sorghum intercropped with soybeans on management of <i>Popillia japonica</i>	105
Abstract	106
Introduction.....	107
Methods	111
Study system	111
Plant Semiochemical Extracts.....	112
Chemical analysis with GC-MS.....	113

Video-tracking Assay with Ethovision	114
Preference Assay	115
Statistical analysis	117
Volatile profiling.....	117
Video-tracking Assay with Ethovision	118
Preference Assay.....	119
Results.....	120
Plant Semiochemical Profiles	120
Video-tracking Assay with Ethovision	1
Preference Assay.....	3
Discussion	6
Chapter 5 - Conclusion	11
Natural land in agricultural landscapes: a help, not a hindrance	11
<i>Popillia japonica</i> : a turf pest, not a grassland pest	13
Agricultural insect communities in changing landscapes and climates.....	15
References.....	17
Appendix A -.....	19
Table A.1: Insect Totals. Insects are identified as pests in red, predators in green, pollinators in blue, and other insects in black. Thrips and whiteflies were not counted as pests due to correlation with leaves in the sweep.	19
Table A.2: Results from the interaction generalized linear mixed-effects model for evaluating the effects of semi-natural land cover (proportion grassland), seasonal precipitation, ecoregion (Glaciated or Cuestas relative to Flint Hills), local edge type (agricultural, road, or semi-natural), and summer maximum temperature on pest abundance. All fixed-effect predictors included in the full models are shown; the random effect of site is not displayed. Significant effects are identified in bold font.	21
Table A.3: Summary of the t-tests for the preference index comparing the control to the treatment in the video-tracking assay coupled with Ethovision for <i>Popillia japonica</i>	22

List of Figures

- Figure 1-1 The Integrated Pest and Pollinator Management pyramid. This pyramid represents the decision structure of IPPM, prioritizing proactive actions at the base of the pyramid with landscape management, and progressing to more in-put based actions only if necessary..... 5
- Figure 2-1 Map of the 30-year normal annual precipitation ranges across Kansas (top left) which is located in the central United States (bottom left), and 30-year normal annual precipitation ranges across our study area with study sites represented by black dots and ecoregions indicated with black circles (right). Precipitation values were derived from the Prism 30-year normal precipitation raster. 29
- Figure 2-2 Percentage of surrounding semi-natural area within a 2-kilometer radius for each field within the study. Semi-natural area included areas identified as grassland, pasture, forest, or wetland in USDA’s annual Cropscape raster for the corresponding study year..... 31
- Figure 2-3 Effect of surrounding grassland cover on insect pest abundance, with grassland shown on its original scale as the proportion of grassland within a 1-km buffer. The solid line represents the model predictions, while the shading indicates 95% confidence intervals. Predictions are presented on the response scale, with all other covariates held at their mean values. 44
- Figure 2-4 Distance-based redundancy analysis (db-RDA) showing the relationship between pest community composition and environmental variables. Environmental vectors represented by gray arrows indicate the direction and relative strength of each variable’s effect on community structure. Sites are represented as points, colored by ecoregion, with ellipses which encompass 95% of sites in that grouping. Species/taxa labels are plotted centered on their db-RDA species score. 45
- Figure 2-5 Effect of surrounding land cover on pollinators with facet panels showing differing effects at low, medium and high precipitation levels. The solid line represents the model predictions, while the shading indicates 95% confidence intervals. Predictions are presented on the response scale, with all other covariates held at their mean values. 47
- Figure 2-6 Distance-based redundancy analysis (db-RDA) showing the relationship between predator community composition and environmental variables. Environmental vectors represented by gray arrows indicate the direction and relative strength of each variable’s

effect on community structure. Sites are represented as points, colored by location, with ellipses which encompass 95% of sites in that grouping. Species/taxa labels are plotted centered on their db-RDA species score.	48
Figure 2-7 Effect of surrounding land cover on pollinators with facet panels showing differing effects at low, medium and high precipitation levels. The solid line represents the model predictions, while the shading indicates 95% confidence intervals. Predictions are presented on the response scale, with all other covariates held at their mean values.	49
Figure 2-8 Distance-based redundancy analysis (db-RDA) showing the relationship between pollinator community composition and environmental variables. Environmental vectors represented by gray arrows indicate the direction and relative strength of each variable's effect on community structure. Sites are represented as points, colored by location, with ellipses which encompass 95% of sites in that grouping. Species/taxa labels are plotted centered on their db-RDA species score.	51
Figure 2-9 Pest (a), predator (b), and pollinator (c) abundance by transect location; center, agricultural edge (AgEdge), road edge (Rd Edge), and natural edge (NatEdge). Boxes show the interquartile range (25th–75th percentiles), with the horizontal line representing the median. Whiskers extend to the most extreme values within 1.5x the interquartile range, and points beyond the whiskers are outliers. Asterisks indicate significant difference from center.	52
Figure 3-1 United States map of Japanese beetle (Jb) infestation status by state. States listed as “Category 1” are uninfested and Jb are considered quarantined pests. “Category 2” are uninfested or partially infested states and Jb are regulated but not quarantined. “Category 3” are partially or generally infested state, and Jb are not regulated. “Category 4” states are not known to be infested. (modified from Japanese Beetle Harmonization Plan, 2022).....	82
Figure 3-2 Comparison of the model prediction values for Japanese beetle presence for 2021 (a) with the actual presence values in 2021 at the county levels (b). For actual presence values, 1 indicates that Japanese beetles were present in the county, 0 indicates that they were absent, and NA indicates that the status was unreported to both data sources.	88
Figure 3-3 Relationships between each land cover and climate variable and Japanese beetle presence/absence shown with a smooth line. The grey shading represents the 95% confidence intervals. The probability of use varies with proportion of developed areas (a),	

proportion of corn and soybean (b), proportion of grassland and pasture (c), annual mean maximum temperature in degrees Celsius (d), annual mean minimum temperature in degrees Celsius (e), and total annual precipitation in mm (f).	89
Figure 3-4 GAM predictions for Japanese beetle suitability per county for 2025 (a) and 2030 (b) under average climate and land cover conditions for 2017 - 2021.	91
Figure 3-5 GAM predictions for Japanese beetle suitability per county under future climate scenarios, for the RCP 2.6 scenario with a temperature increase of 1°C and a 10% increase in precipitation (a) and the RCP 8.5 scenario with a temperature increase of 4°C and a 10% decrease in precipitation (b) and average land cover conditions for 2017 - 2021.	92
Figure 4-1 Layout of the field plot; intercropped soybean plants were planted directly next to sorghum, while monocropped soybean plants were surrounded by soybean.	112
Figure 4-2 Video tracking assays with Ethovision (a) were conducted in a petri dish with a treatment extract on one side and a control extract on the other side. Each stimulus had a defined stimulus zone and a treatment side. Groups of <i>P. japonica</i> were released in dual choice assays (b) and recaptured after 1 h and 24 h. Dual choice assays had 5 zones, with treatments of fresh plant cuttings in zones 1 and 5.	117
Figure 4-3 Non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis similarities among plant semiochemical extracts from intercropped soybean (inter-soy), monocropped soybean (mono-soy), soybean-sorghum mix (mix), and sorghum. Points represent individual samples, colored by treatment. Ellipses indicate 95% confidence intervals around group centroids. The stress value was 0.04.	121
Figure 4-4 Six compounds from the plant semiochemical extracts were associated with significant differences between treatments, including 1-octen-3-ol (a), nonanoic acid (b), indane (c), 2,4-Di-tert-butylphenol (d), 1-octanol (e), and Dodecane-1-iodo (f). Abundances of each compound across all samples by treatments are shown as boxplots in ng g-1 with thick horizontal lines representing medians, boxes representing the interquartile ranges, and whiskers representing the ranges. Abbreviations: mono soy = monocropped soy, inter soy = intercropped soy, mix= soy-sorghum-mix.	122
Figure 4-5 Comparisons of <i>P. japonica</i> behaviors within video-tracking assays shown as the difference between treatment and control values (log values for latency). Behaviors include (a), frequency of entries into the treatment stimulus zone (b), latency to finding the	

treatment stimulus zone (c), and mobility (d). Points indicate individual responses, center lines represent group medians, boxes represent interquartile ranges, and black dots indicate outliers. Abbreviations: mono soy = monocropped soy, inter soy = intercropped soy, mix= soy-sorghum-mix. 2

Figure 4-6 Proportion of beetles (n=28) found in each zone between two treatments found on opposite ends of a release-recapture dual choice assay after 1 h (a) and 24 h (b). Zones 1 and 5 included the treatment plants, while zones 2 and 4 indicate preference for either treatment. NR values indicate the rate of non-responders. Beetles who stayed in the center release zone (zone 3) or buried themselves in the peat moss were considered non-responders. 4

List of Tables

Table 2-1 Description of candidate interaction models to clearly show differences between the interaction and fixed effect variables within in each of the candidate models used to test if interactions improved model fit over the additive model.	39
Table 2-2 Results from the most parsimonious additive or interaction generalized linear mixed-effects models evaluating the effects of semi-natural land cover (proportion grassland or total semi-natural land), seasonal precipitation, ecoregion (Glaciated or Cuestas relative to Flint Hills), local edge type (agricultural, road, or semi-natural), and summer maximum temperature on (1) pest abundance, (2) predator abundance, and (3) pollinator abundance. All fixed-effect predictors included in the full models are shown; the random effect of site is not displayed. Significant effects are identified in bold font. Effects of categorical variables are shown as model coefficients relative to the reference level (field center for location, and Flint Hills for ecoregion). The overall effect of ecoregion was evaluated using likelihood ratio tests and Tukey-adjusted post-hoc comparisons (see Results).	43
Table 3-1 Model relationships between Japanese beetle occurrences and climate and land cover variables ($r^2 = 0.692$).	88
Table 3-2 Model relationships between Japanese beetle occurrences and state and year ($r^2 = 0.692$).	90
Table 4-1 Simper results identifying compounds responsible for the differences between treatments	123
Table 4-2 Compounds identified by SPME-GC/MS from extracts of monoculture soybean, intercropped soybean, mized soybean and sorghum, and sorghum alone. Means $\pm$ SE represent compounds in ng g ⁻¹ dry biomass (shaded from low values in browns to high values in blue-greens)	1
Table 4-3 Summary of the emmeans pairwise contrasts for comparing treatment preference in the release-recapture dual-choice assay for <i>Popillia japonica</i>	5

Acknowledgements

I would like to express my heartfelt thanks to the many people who supported me throughout the course of this research and my graduate studies. This dissertation would not have been possible without their guidance, encouragement, and generosity of time and expertise.

First and foremost, I am deeply grateful to my advisor, Dr. Tania Kim, for her mentorship, patience, and unwavering support. Her guidance shaped not only this dissertation but also my development as a scientist. I greatly appreciate the opportunities she provided, as well as her encouragement to think critically and independently throughout this process. Dr. Kim provided me with not only the tools but the people that I needed to help me on this journey. From suggesting the best classes to hiring the greatest undergraduate helpers, Dr. Kim connected me to the supportive community I needed to grow and thrive. She encouraged me to acquire a variety of skills and view my projects through multiple lenses. She pushed me out of my comfort zone into new realms of discovery that I have come to truly enjoy. Although we may wish for it to be neat, Dr. Kim has taught me to appreciate that science is messy, and it takes a lot of digging to uncover the true mechanisms and understanding. Each experiment is just one piece of the puzzle.

I would also like to thank my committee members, Dr. Brian McCornack, Dr. Kate Nelson, and Dr. Brian Spiesman, for their insightful feedback, thoughtful discussions, and valuable suggestions that strengthened this work. I am grateful to Dr. Kate Nelson for her guidance in spatial analysis, programming, and data cleaning, and for helping me think more rigorously about how to translate ecological processes into quantitative frameworks. I thank Dr. Brian McCornack for his expertise in applied ecology and integrated pest management, and for providing valuable insight into how these ideas translate into real-world agricultural systems. I am grateful to Dr. Brian Spiesman for his thoughtful discussions on metapopulation theory and

landscape ecology, and for consistently pushing me to think more creatively about spatial processes and ecological mechanisms.

I am grateful to the members of the Kim Insect Ecology Lab for their support, collaboration, and camaraderie. In particular, I thank Kaitlin Schieuer, Gus Brunette, Maggie Anderson, Skyler Morais, Chad Zerr, Olivia Jarboe, and Fabel Yanez for their assistance in the field and lab, as well as for the many helpful conversations and shared experiences along the way. I am also grateful to Dr. Rob Morrison and Dr. Alison Gerken for their collaboration and guidance in my behavioral and chemical ecology research. This chapter would not have been possible without the tremendous support of the Morrison Lab, especially Dr. Rob Morrison, Dr. Matt Hetherington, and Kealani Simpson. I would also like to thank my excellent professors who helped me grow my skills and subject knowledge needed to complete this research, especially Dr. Dan Sullins, Dr. Keith Gido, and Dr. Tom Phillips. I am also grateful to my Master's advisor, Dr. Kevin Matteson, for his encouragement to pursue my PhD and his continued support.

One of the most rewarding experiences during my PhD has been the opportunity to be a FFAR Fellow in the 2023-2026 cohort. I am so grateful for the community of interdisciplinary scholars and professional development opportunities it has provided, which have meaningfully shaped my growth as a scientist and as a person. I am deeply indebted to Dr. Rebecca Dunning, our fearless leader and guide to the world of soft skills. I especially thank my two mentors, Dr. Alison Gerken and Stephanie Darnell, for generously sharing their time, guidance, and good vibes with me over the past several years. Their thoughtful, supportive, and steadfast advice has been instrumental throughout this journey.

To the soybean growers that let me into their fields, drove me around in their trucks and gators, and texted with me throughout the summer about bugs, thank you. I also would like to

thank the Kansas Soybean Commission, whose financial assistance made this research possible. Additional thanks go to the Kansas State Entomology Department for providing resources and a supportive academic environment.

Finally, I would like to thank my family and friends for their unwavering encouragement and patience throughout this journey. Their support provided balance, perspective, and motivation during both the challenging and rewarding moments of graduate school. I am especially grateful to Anton Kuchеров for his constant encouragement and belief in me. To our two children, Alex and Michael, thank you for your patience with me as I balance work and family and for the endless joy and laughter you bring to my life.

Dedication

This dissertation is dedicated to my grandmother, Norma P. Dumais, who inspired my love of insects, amphibians, birds, trees, weeds, and the natural world. I am forever grateful for the thousands of hours spent exploring her backyard and the freedom it gave me to question, wonder, and appreciate. Stay curious.

Chapter 1 - Introduction

Climate and land use change are negatively affecting pest dynamics in agroecosystems and threatening food security (Bianchi et al. 2006, Rusch et al. 2016, Deutsch et al. 2018, Lehmann et al. 2020, Pereira et al. 2025). One major threat to global crop yield is agricultural pests, and agricultural intensification has led to increased pesticide usage with negative effects on non-target species including beneficial insects (Thurman et al. 2017), human health (Elahi et al. 2019), and insecticide resistance (Khodaverdi et al. 2016, Hough et al. 2017). The negative impacts of agricultural intensification coincide with an unprecedented global decline in insect species (Cardoso et al. 2020, Wagner et al. 2021). These declines are not only occurring amongst the specialist species, but even common generalist species (van Klink et al. 2024). With a loss of insect abundance and richness, we also see declines in ecological functioning, leading to a loss of ecosystem services provided by those insects, including pollination, predation, nutrient cycling, and wildlife nutrition.

A study on the main drivers of insect biodiversity loss identified the following causes, in order of importance; (i) habitat loss and conversion, (ii) pesticides and fertilizers, (iii) pathogens and introduced species, and (iv) climate change (Sánchez-Bayo and Wyckhuys 2019).

Agricultural intensification is a large contributor to habitat loss and fragmentation as well as pesticide and fertilizer pollution, and agricultural land accounts for nearly half of all of Earth's habitable land (Ritchie and Roser 2019). Therefore, to conserve insect biodiversity and ecosystem services, we need to rethink how we manage the world's agricultural lands (Forister et al. 2019) while maintaining agricultural productivity to meet growing food needs. Unfortunately, conservation and agricultural production are often viewed as competing rather than

complimentary. Biodiversity conservation compliments agricultural production as pollinator and natural enemy abundance and richness lead to an increase in ecosystem services (Dainese et al. 2019). However, farmers are often more likely to think of conserving natural land for insect biodiversity as a pest risk than to see conservation of insect biodiversity as helpful. Studies have shown that farmers are more likely to be able to identify pest insects than beneficial insects (Teixeira et al. 2025), underestimate the value of biological control, especially by insect and arachnid predators, and are unaware of the indirect benefits of insect predators as biological control on quality and yield (Martínez-Sastre et al. 2020).

Land use change is a driver of insect biodiversity loss and has negative consequences for ecosystem services because it creates pressure and imbalance within ecological systems through mechanisms such as habitat loss, habitat conversion, or landscape simplification where a landscape becomes more homogeneous (Sánchez-Bayo and Wyckhuys 2019). Landscape simplification is often due to the conversion of natural habitats to agricultural land or urban areas. Beneficial insects such as pollinators and natural enemies rely on additional resources from these natural habitats, so landscape simplification reduces their species richness and abundance (Dainese et al. 2015). Because beneficial insects are more likely to rely on these resources than agricultural pests, this can lead to a trophic decoupling of predators and prey. Rusch et al (2016) found a consistent negative effect of the proportion of cropland within 1 km on natural pest control of aphids with pest control being 46% lower on average in fields within cropland dominated landscapes.

Landscape simplification can also lead to an increased need for pesticides, further harming insect communities and causing further negative trophic effects. In the Midwest, Meehan et al. (2011) found that the proportion and patch size of cropland increased the usage of

insecticides. Additionally, the pesticides applied to cropland are detrimental to beneficial insects, threaten human health, and can even affect environmental health, such as water quality.

Furthermore, as pesticide usage increases, targeted pest insects are becoming resistant, and fields require more pesticide or higher toxicity pesticide than in previous years (DiBartolomeis et al. 2019). This can lead to instability within the insect communities, where pests are resistant, but predators are not, or predators are not present in adequate abundances when new populations of pests move in from neighboring fields.

In the late 1950s, after the boom of organosynthetic insecticides, concern arose about the risk of overuse of insecticides. Similar issues with pesticides were becoming apparent then; “resistance, resurgence of primary pests, upsurges of secondary pests, and overall environmental contamination” (Kogan 1998). These concerns led to the rise of the integrated control concept, now known as IPM. Originally, IPM had its basis in ecological theory, with the first principle of IPM being the need to consider the total ecosystem (Kogan, 1998). Despite these good intentions, IPM has stayed field-scale focused and input-driven rather than incorporating the envisioned attention to agroecosystem functions and ecosystem services (Deguine et al. 2021).

The failure to integrate landscape-level, ecosystem service based approaches into mainstream IPM stems from a variety of road blocks including; risk aversion and a disproportionate emphasis on losses from pest-related damages and worse-case scenarios, costly monitoring schemes and a lack of knowledge about decision thresholds for many crops, and extensive lobbying and corporate involvement in policy (Deguine et al. 2021). Additionally, landscape-ecology based IPM is inherently context-dependent as it operates across many trophic levels and depends on multiple spatial scales. As a result, we see that the literature is dominated by inconsistent outcomes across crop and habitat types, insect trait groups, and geographic areas

(Begg et al. 2017). Simply put, farmers continued to use field-level agrochemical inputs for their ease-of-use, cost-effectiveness, and visible pest protection in the short term. As pest management has pivoted its focal point to genetically engineered plant resistance, RNAi, and treated seed (Dara 2019), some entomologists emphasize the renewed importance of landscape-level management. Proactive management at the landscape and farm level have been a centerpiece of Agroecology and Integrated Pest and Pollinator Management with methods that prioritize natural enemies and pollinators at a larger spatial scale for a more conservation-based approach (Lundin 2021, Deguine et al. 2021).

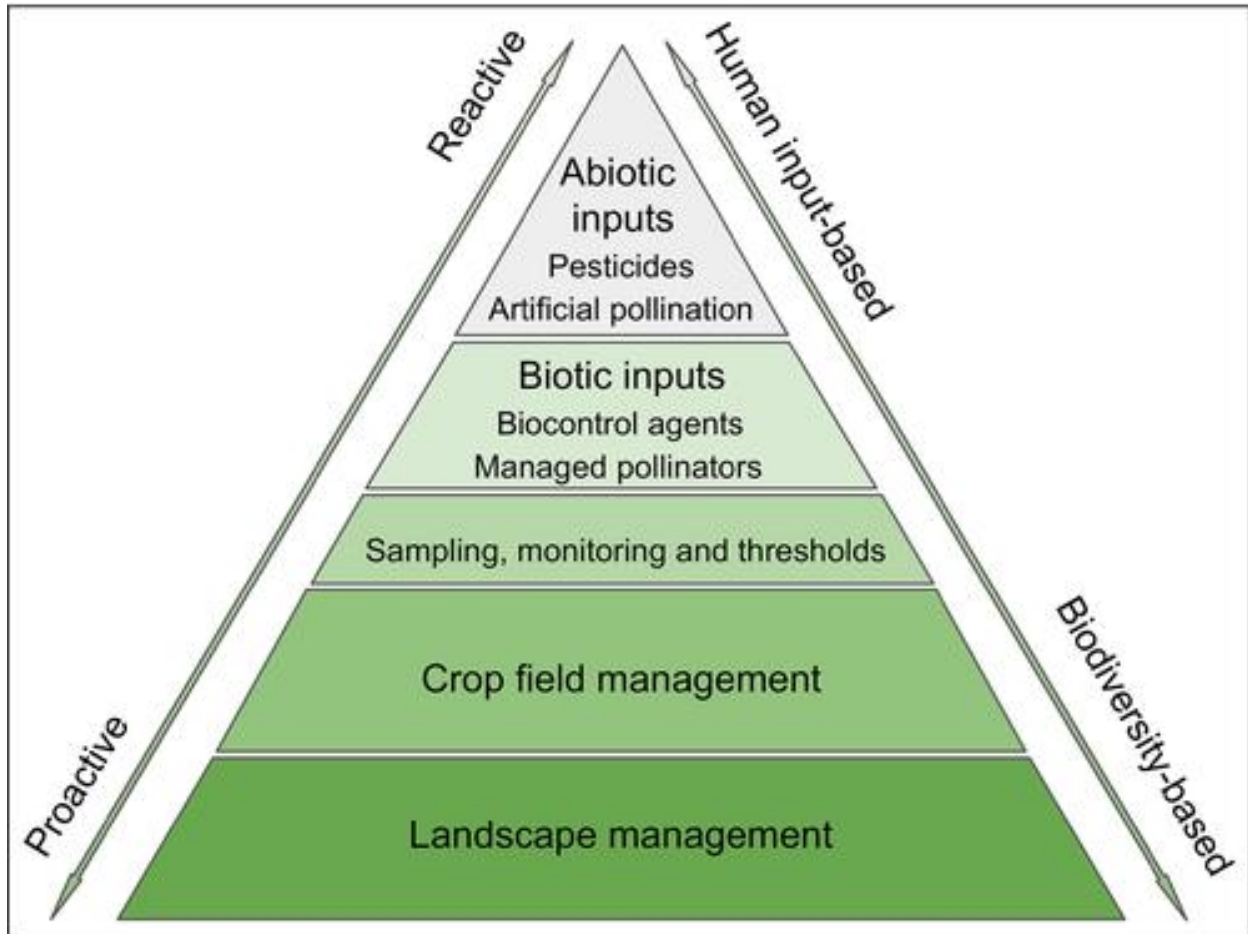


Figure 1-1 The Integrated Pest and Pollinator Management pyramid. This pyramid represents the decision structure of IPPM, prioritizing proactive actions at the base of the pyramid with landscape management, and progressing to more in-put based actions only if necessary.

A landscape approach

Proactive measures to reduce pests and promote pollinators include considering the broader landscape, i.e. Figure 1 (Lundin 2021). Landscapes are heterogeneous areas that can range from tens of centimeters to hundreds of kilometers, depending on the habitat requirements of the focal organism (Levin 1992). For insect species, the size of the relevant landscape often varies from meters to kilometers and is determined by body size and dispersal capabilities (Steffan-Dewenter et al. 2002). The landscape composition of areas surrounding agricultural

fields could impact a pest's abundance either directly through its dispersal, mortality and reproduction, or indirectly by affecting its natural enemies (Tscharntke et al. 2012). As such, landscape effects are inherently context-dependent because individual species' traits guide how organisms perceive and interact with their environment. While natural areas in the surrounding landscape would likely have negative effects on species that are agricultural specialists, species that overwinter in natural areas may benefit from natural land in the surrounding landscape (Tscharntke et al. 2012). Insects such as pollinators and natural predators require support at a landscape scale to provide nesting areas, overwintering habitat, and seasonal flowers (Bianchi et al. 2006). Thus, increasing plant diversity and adding sections of natural and semi-natural habitat can attract both natural enemies and pollinators to agroecosystems through added resources (Egan et al. 2020, Lundin 2021). However, certain pest species can also benefit from the resources of surrounding semi-natural land (Carsten Thies et al. 2005; Martin et al. 2013; John M Holland et al. 2016; Akter et al. 2023).

From a metacommunity perspective, we can think of habitat patches within the short-term dispersal ranges of the organisms being studied as a network of populations. These habitat patches can be colonized from regional species pools across nearby habitat patches, and the diversity available within this range strongly influences within-patch species richness (Hanski 1998). Complex landscapes, landscapes with many land cover types, support higher species diversity than simple landscapes and therefore may provide a more diverse species pool of colonizers for patches within the landscape (Tscharntke et al. 2005). These resources may be more important for natural predators than for pests, leading to differences in species richness or abundance. For example, complex landscapes (landscape Shannon diversity) were positively

correlated with lacewing abundance, but not thrip abundance in orchards (Wen et al. 2024), which could lead to decoupling of trophic levels between thrips and their lacewing predators.

Spillover of organisms into agroecosystems from nearby natural habitats has been well-documented (Thies and Tschardtke 1999, Bianchi et al. 2006, Blitzer et al. 2012) and one explanation for this movement is exploitation of resources from the different patches. For example, parasitoids (Landis et al. 2000) and pollinators such as butterflies (Steffan-Dewenter and Tschardtke 1997) and bees (Klein et al. 2003, Holzschuh et al. 2006) may require resources from different patches for nesting, hostplants, nectar and prey (Tschardtke et al. 2012). In simplified landscapes, community dynamics are likely determined by the species pool within the natural remnants of the surrounding landscape (Bengtsson 2009). Previous studies have found evidence that higher amounts of natural area in the surrounding landscape correlates with increased regulation of specific pests by specific predators. Veres et al. (2013) performed an analysis of the scientific literature to assess how the proportion of different land covers at the landscape level is related to the abundance of pests or to their control by natural enemies. In 45 out of 72 independent case studies, landscapes with higher proportions of semi-natural areas had lower pest abundance or higher pest control in fields. Liere et al. (2015) looked at biological control of soybean aphids and found that landscapes with a higher diversity of habitats resulted in more natural enemies, fewer aphids, and, in some cases, a greater soybean yield.

As insects navigate through landscapes, they must make navigational choices based on their observations. Insects use various sensory mechanisms to navigate, including visual orientation, chemosensory perception, mechanosensory cues, and auditory cues. Their ability to move from one habitat patch into another depends on whether or not the novel patch is within that species' perceptual range; the distance at which an organism is able to locate a suitable

habitat patch, and it varies by species (Wiens 1989, Zollner 2000). Successful navigation to a novel patch depends on both the organisms ability to identify the patch through their sensory mechanisms and the patch's location in relation to the organism's position (MacDonald et al. 2019). Mitchell et al. (2014) found consistent evidence that arthropod abundance and diversity are strongly affected by landscape structure, particularly by the presence of field margins and forest fragments. More recent global syntheses confirmed these patterns but emphasize their context dependence (Karp et al. 2018, Dainese et al. 2019). Thus, we see that landscape composition and structure can play a strong role in pest management for agricultural fields.

Increasing natural land cover proportions in agricultural landscapes does not seem to consistently increase biological control or decrease pests across studies, likely due to the complex nature of these multi-scale interactions between pests, predators, and habitat. In a global study by Karp et al. (2018), although landscape composition did explain variance within individual studies, there were differing responses across the studies by both pests and predators. Analyzing the responses by insect traits and crop variability helped to explain some of the inconsistencies and suggested the use of a portfolio of strategies for the management of complex, changing insect communities (Tamburini et al. 2020). More recent work with this dataset shows that considering multiple scales of landscape composition in addition to insect traits, trophic interactions, and crops traits helps to further explain this variation, highlighting the importance of a multi-scale approach (Poveda et al. 2025). However, the authors state that more research is needed to clarify how conservation of natural lands within agroecosystems affects entire insect communities within agricultural fields across spatial and temporal scales (Poveda et al. 2025). If we are to increase biodiversity through merging conservation and agriculture in agroecosystems and agri-environment schemes (Kremen and Merenlender 2018), then we need to have a more

comprehensive understanding of the interacting landscape and climatic effects on agricultural insect communities and how insects are navigating to fields within these landscapes.

Climate influences and invasive species dynamics in a changing world

Predicted changes in temperature and weather patterns will further complicate our ability to accurately predict and respond to pest outbreaks across agricultural landscapes. Climate variables such as temperature and precipitation affect the life cycles, survival, and spread of pest insects (Thomson et al. 2010, Jactel et al. 2012, Eigenbrode et al. 2015, Skendžić et al. 2021). These same climatic variables also affect relationships between pests and their natural enemies (Prakash et al. 2014, Thurman et al. 2017, Urbaneja-Bernat et al. 2019). Climatic and landscape effects are often thought of as additive effects; that both land cover and climate will affect pest population dynamics. However, it is important to consider that they may have interactive effects as well. For example, higher precipitation levels can result in higher amounts of vegetative growth and floral resources, while low precipitation or drought can lead to the desiccation of nesting and supplementary nutrition resources provided by the natural land cover in the landscape. Changes in levels of precipitation and temperature, as well as their timing, may lead to phenological variation of floral resources available in the landscape, either amplifying or reducing the effect of natural areas within the landscape. These interactions are difficult to identify because they required replicated data sets across large gradients of both climate and land cover. Identification of interactions is complicated because climate and land cover are often correlated, i.e. more agricultural land in warmer, wetter climates.

Invasive species are a particularly problematic subset of agricultural pests, causing a reduction in food supply with global costs of \$279 billion USD in 2019 (Roy et al. 2024), and their impact is expected to rise with increased global trade (Paini et al. 2016) and climate change (Skendžić et al. 2021). Therefore, understanding how climate and land use intensification interact to affect agricultural insect community dynamics and the impact of invasive species is essential to predict which areas are vulnerable to increased pest pressure and target management efforts. By nature of being invasive, these species are spreading across wide spatial scales while their presence and abundance increase with time. In studying their habitat use and associated risk, we need to again consider multiple scales and the possibility of variation across different regions and habitats. How they spread in one region may not extrapolate accurately to a new region with different land cover types or climatic ranges.

Soybean: a dominant land cover in the central U.S. landscape

Soybean (*Glycine max*) is one of the most important agricultural crops in the world. Soybean is grown for its seeds which are primarily used for human food, animal feed, and cooking oil. The United States is one of the world's top producers of soybeans, along with Brazil, and more than 80% of U.S. soybean is grown in the Midwest (Economic Research Service 2025). Soybean is the second most planted crop in the United States by acreage, with 83.4 million acres planted in 2025 (National Agricultural Statistics Service 2025) and generating \$124 billion annually (Checkoff 2023). It is a close second to corn (*Zea mays*), of which 95.2 million acres were planted in 2025, and nearly double the acreage for wheat (*Triticum aestivum*) which covered 45.5 million acres in 2025 (National Agricultural Statistics Service 2025). Land

use in the Midwest is dominated by cropland (51%), followed by grassland and pasture (41%) (Winters-Michaud 2024). The Midwest's Northern Great Plains temperate grassland ecosystem is one of the most endangered and least protected ecosystems on earth, and factors such as land conversion have led to a loss of 62% of North American temperate grasslands (Monnett and Stone 2025). To conserve the remaining grassland, private landowners will need to see the value in setting aside natural land in areas dominated by cropland.

***Popillia japonica* Newman: a landscape pest**

Taking a landscape point of view for pest management is especially important with insects that disperse over long distances and utilize different land covers throughout their life cycle. The Japanese beetle (*Popillia japonica* Newman) is a good example of this type of pest. *Popillia japonica* is an invasive species that feeds on over 300 plant species, including soybean, corn, and other field crops (Fleming 1972, Potter and Held 2002, Shanovich et al. 2019). After introduction to the United States in 1916, *P. japonica* spread west across the United States and by 1998, they had infested all states east of the Mississippi river (Kistner-Thomas 2019). By 2015, there were moderate populations west of the Mississippi River (Kistner-Thomas 2019). In the Midwestern United States, the potential of *P. japonica* to damage corn and soybean production is particularly concerning (Shanovich et al. 2019). *P. japonica* can cause severe damage if they defoliate soybean leaves during a reproductive stage (e.g., approximately 20% yield loss after 30% defoliation (Hammond 1994). In corn, *P. japonica* interfere with pollination when they clip the silks which causes a reduction of kernels (Edwards 1999).

Currently, the main way to manage *P. japonica* populations in field crops is to spray pesticides such as pyrethroids and neonicotinoids. This is not efficient because *P. japonica*

disperse over long distances, arriving to fields from other areas in the landscape, and fields are quickly reinfested by new immigrating populations of *P. japonica* (Potter et al. 2006, Shanovich et al. 2019). One study of *P. japonica* movement found that within a 24 hr time period, the majority of marked individuals moved 5–9 km, with one individual traveling 12 km (Lessio et al. 2021). In a case such as this, we need to consider the entire landscape when we evaluate a field's risk of infestation and when considering control methods. We should also consider how *P. japonica* individuals perceive habitat patches within a landscape and navigate to a field.

Multi-scale Integrated Pest Management

In my dissertation work, I explored the effects of landscape composition and climate on insect communities within soybean fields and then focused specifically on the invasive insect pest *P. japonica* across multiple scales from how it spreads across a novel landscape to how it interacts with soybean through behavioral processes. Insects interact with their environments across multiple scales, which can cause significant issues when we try to manage them only on a field level. For example, individual *P. japonica* beetles disperse up to 12 km, forage within a 2 km scale (Lessio et al. 2021), and feed at the scale of an individual plant. Therefore, we need to consider multiple scales when we manage insect populations.

First, I analyzed the effects of semi-natural land in the surrounding landscape and climate, as well as their interaction, on insect communities at a field scale. Kansas offers a rare opportunity to explore these interactions due to its unique precipitation gradient and the large amount of grassland preserved in the Flint Hills. The objective of this study was to analyze the additive and interactive effects of natural land cover in the surrounding landscape and (i) precipitation, (ii) temperature, and (iii) landscape configuration in the form of bordering field

types on pest, predator, and pollinator insect abundances. By exploring these effects within one system in an area with a strong precipitation gradient and a large amount of natural land, we can see how semi-natural land in the surrounding landscape affects pest, predator, and pollinator populations in the field, and how that changes across a range of climatic conditions. Another objective of this study was to explore how these different variables affected the composition of insect communities. This knowledge expands our understanding of the impact on conserving natural land within agroecosystems and has important management applications for integrated pest management, especially in a changing climate.

Then, I focused on the regional invasion dynamics of an invasive insect pest, *P. japonica*, that utilizes multiple land cover types, feeding on grass roots as larvae and then agricultural crops as adults (Potter and Held 2002). Existing risk maps for *P. japonica* in the Central United States were based on global citizen science observations and differed in their predictions; with one predicting most of the Great Plains would have lower suitability but suggesting that the managed grasslands would further increase suitability (Kistner-Thomas 2019) and another predicting that the area would be largely unsuitable (Borner et al. 2023). The main objectives of this study were to (i) clarify regional habitat associations and suitability predictions for *P. japonica* spread in the Midwest and Great Plains through models trained with robust regional datasets and (ii) incorporate the factor of time at the leading edge of an invasion. By aggregating observations from citizen science data with monitoring data from State Agricultural Departments and University Cooperative Extension Agencies, I was able to capture not only developed areas where citizen scientists spend their time, but also private land and agricultural land where growers reported *P. japonica* sightings or they had been trapped through monitoring efforts. With this integrated, robust dataset, I modeled climate and habitat associations over time and

created regional risk maps for the future spread of *P. japonica* in the American Midwest and Great Plains. This regional approach to invasive species risk mapping resulted in a more tailored risk map which accounts for environmental variation and reduces extrapolation in comparison to global predictions.

With county-by-county risk maps, landowners can see what the broad scale risk is for *P. japonica* in their area, and our field-scale study showed that natural grasslands in the surrounding area decreases pest abundance, including *P. japonica*, but landowners cannot control their neighbors. Therefore, they will need ways to deter this landscape-level pest from their fields. One integrated pest management strategy to reduced abundance of *P. japonica* in soybean fields is to intercrop soybean with sorghum. The original study's authors suggested that this effect may be mediated by behavioral processes in response to semiochemicals, but they did not test this. So, on a plant-insect scale, I analyzed a possible semio-chemical mechanism for the effects of intercropping on *P. japonica* populations. In this experiment, we compared the behavioral response of *P. japonica* to extracts from intercropped soybean, monocropped soybean, and a mixture of soybean and sorghum to uncover if intercropping soybean with sorghum disrupts olfactory cues to which *P. japonica* respond. The objectives of this study were as follows; (i) identify possible differences in the semiochemical profiles of intercropped and monocropped soybean, (ii) evaluate the effect of these semiochemicals on movement by *P. japonica* individuals, and (iii) evaluated *P. japonica* group preference in a dual-choice, release-recapture assay. These findings help us to more efficiently monitor and respond to advancing populations of *P. japonica* in the agricultural heart of the United States.

References

- Begg, G. S., S. M. Cook, R. Dye, M. Ferrante, P. Franck, C. Lavigne, G. L. Lövei, A. Mansion-Vaquie, J. K. Pell, S. Petit, N. Quesada, B. Ricci, S. D. Wratten, and A. N. E. Birch. 2017. A functional overview of conservation biological control. *Crop Protection* 97:145–158.
- Bengtsson, J. 2009. Chapter 9 Applied (meta)community ecology: diversity and ecosystem services at the intersection of local and regional processes. Page 0 *in* H. A. Verhoef and P. J. Morin, editors. *Community Ecology: Processes, Models, and Applications*. Oxford University Press.
- Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings. Biological Sciences* 273:1715–1727.
- Blitzer, E. J., C. F. Dormann, A. Holzschuh, A.-M. Klein, T. A. Rand, and T. Tscharntke. 2012. Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment* 146:34–43.
- Borner, L., D. Martinetti, and S. Poggi. 2023. A new chapter of the Japanese beetle invasion saga: predicting suitability from long-invaded areas to inform surveillance strategies in Europe. *Entomologia Generalis*:951–960.
- Cardoso, P., P. S. Barton, K. Birkhofer, F. Chichorro, C. Deacon, T. Fartmann, C. S. Fukushima, R. Gaigher, J. C. Habel, C. A. Hallmann, M. J. Hill, A. Hochkirch, M. L. Kwak, S. Mammola, J. Ari Noriega, A. B. Orfinger, F. Pedraza, J. S. Pryke, F. O. Roque, J. Settele, J. P. Simaika, N. E. Stork, F. Suhling, C. Vorster, and M. J. Samways. 2020. Scientists' warning to humanity on insect extinctions. *Biological Conservation* 242:108426.
- Dainese, M., D. I. Luna, T. Sitzia, and L. Marini. 2015. Testing scale-dependent effects of seminatural habitats on farmland biodiversity. *Ecological Applications* 25:1681–1690.
- Dainese, M., E. A. Martin, M. A. Aizen, M. Albrecht, I. Bartomeus, R. Bommarco, L. G. Carvalheiro, R. Chaplin-Kramer, V. Gagic, L. A. Garibaldi, J. Ghazoul, H. Grab, M. Jonsson, D. S. Karp, C. M. Kennedy, D. Kleijn, C. Kremen, D. A. Landis, D. K. Letourneau, L. Marini, K. Poveda, R. Rader, H. G. Smith, T. Tscharntke, G. K. S. Andersson, I. Badenhausser, S. Baensch, A. D. M. Bezerra, F. J. J. A. Bianchi, V. Boreux, V. Bretagnolle, B. Caballero-Lopez, P. Cavigliasso, A. Četković, N. P. Chacoff, A. Classen, S. Cusser, F. D. da Silva e Silva, G. A. de Groot, J. H. Dudenhöffer, J. Ekroos, T. Fijen, P. Franck, B. M. Freitas, M. P. D. Garratt, C. Gratton, J. Hipólito, A. Holzschuh, L. Hunt, A. L. Iverson, S. Jha, T. Keasar, T. N. Kim, M. Kishinevsky, B. K. Klatt, A.-M. Klein, K. M. Krewenka, S. Krishnan, A. E. Larsen, C. Lavigne, H. Liere, B. Maas, R. E. Mallinger, E. Martinez Pachon, A. Martínez-Salinas, T. D. Meehan, M. G. E. Mitchell, G. A. R. Molina, M. Nesper, L. Nilsson, M. E. O'Rourke, M. K. Peters, M. Plečaš, S. G. Potts, D. de L. Ramos, J. A. Rosenheim, M. Rundlöf, A. Rusch, A. Sáez, J. Scheper, M. Schleuning, J. M. Schmack, A. R. Sciligo, C. Seymour, D. A. Stanley, R.

- Stewart, J. C. Stout, L. Sutter, M. B. Takada, H. Taki, G. Tamburini, M. Tschumi, B. F. Viana, C. Westphal, B. K. Willcox, S. D. Wratten, A. Yoshioka, C. Zaragoza-Trello, W. Zhang, Y. Zou, and I. Steffan-Dewenter. 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances* 5:eaax0121.
- Dara, S. K. 2019. The New Integrated Pest Management Paradigm for the Modern Age. *Journal of Integrated Pest Management* 10.
- Deguine, J., J.-N. Aubertot, R. J. Flor, F. Lescourret, K. Wyckhuys, and A. Ratnadass. 2021. Integrated pest management: good intentions, hard realities. A review. *Agronomy for Sustainable Development* 41.
- Deutsch, C. A., J. J. Tewksbury, M. Tigchelaar, D. S. Battisti, S. C. Merrill, R. B. Huey, and R. L. Naylor. 2018. Increase in crop losses to insect pests in a warming climate. *Science* 361:916–919.
- DiBartolomeis, M., S. Kegley, P. Mineau, R. Radford, and K. Klein. 2019. An assessment of acute insecticide toxicity loading (AITL) of chemical pesticides used on agricultural land in the United States. *PloS One* 14:e0220029.
- Economic Research Service. 2025. Soybeans and Oil Crops - Oil Crops Sector at a Glance. United States Department of Agriculture.
- Edwards, C. R. 1999. Japanese Beetle. Pages 90–91 *Handbook of corn insect pests*. K.L. Steffey, M.E. Rice, J. All, D.A. Andow, M.E. Gray, and J.W. van Duyn (eds.). Entomological Society of America, Lanham, MD.
- Egan, P. A., L. V. Dicks, H. M. T. Hokkanen, and J. A. Stenberg. 2020. Delivering Integrated Pest and Pollinator Management (IPPM). *Trends in Plant Science* 25:577–589.
- Eigenbrode, S., T. Davis, and D. Crowder. 2015. Climate change and biological control in agricultural systems: Principles and examples from North America. Pages 119–135.
- Elahi, E., C. Weijun, H. Zhang, and M. Nazeer. 2019. Agricultural intensification and damages to human health in relation to agrochemicals: Application of artificial intelligence. *Land Use Policy* 83:461–474.
- Fleming, W. E. 1972. Biology of the Japanese beetle. Technical Bulletin, Agricultural Research Service, USDA.
- Forister, M. L., E. M. Pelton, and S. H. Black. 2019. Declines in insect abundance and diversity: We know enough to act now. *Conservation Science and Practice* 1:e80.
- Hammond, R. B. 1994. Japanese beetle. Pages 64–65 *Handbook of soybean insect pests*. L. G. Higley and D. J. Boethel (eds.). Entomological Society of America, Lanham, MD.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.

- Holzschuh, A., I. Steffan-Dewenter, D. Kleijn, and T. Tscharntke. 2006. Diversity of flower-visiting bees in cereal fields: Effects of farming system, landscape composition and regional context. *Journal of Applied Ecology* 44:41–49.
- Hough, A. R., J. R. Nechols, B. P. McCornack, D. C. Margolies, B. K. Sandercock, D. Yan, and L. Murray. 2017. The effect of temperature and host plant resistance on population growth of the soybean aphid biotype 1 (Hemiptera: Aphididae). *Environmental Entomology* 46:58–67.
- Jactel, H., J. Petit, M.-L. Desprez-Loustau, S. Delzon, D. Piou, A. Battisti, and J. Koricheva. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology* 18:267–276.
- Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, L. Hunt, A. E. Larsen, A. Martínez-Salinas, M. E. O'Rourke, A. Rusch, K. Poveda, M. Jonsson, J. A. Rosenheim, N. A. Schellhorn, T. Tscharntke, S. D. Wratten, W. Zhang, A. L. Iverson, L. S. Adler, M. Albrecht, A. Alignier, G. M. Angelella, M. Zubair Anjum, J. Avelino, P. Batáry, J. M. Baveco, F. J. J. A. Bianchi, K. Birkhofer, E. W. Bohnenblust, R. Bommarco, M. J. Brewer, B. Caballero-López, Y. Carrière, L. G. Carvalheiro, L. Cayuela, M. Centrella, A. Četković, D. C. Henri, A. Chabert, A. C. Costamagna, A. De la Mora, J. de Kraker, N. Desneux, E. Diehl, T. Diekötter, C. F. Dormann, J. O. Eckberg, M. H. Entling, D. Fiedler, P. Franck, F. J. Frank van Veen, T. Frank, V. Gagic, M. P. D. Garratt, A. Getachew, D. J. Gonthier, P. B. Goodell, I. Graziosi, R. L. Groves, G. M. Gurr, Z. Hajian-Forooshani, G. E. Heimpel, J. D. Herrmann, A. S. Huseeth, D. J. Inclán, A. J. Ingrao, P. Iv, K. Jacot, G. A. Johnson, L. Jones, M. Kaiser, J. M. Kaser, T. Keasar, T. N. Kim, M. Kishinevsky, D. A. Landis, B. Lavandero, C. Lavigne, A. Le Ralec, D. Lemessa, D. K. Letourneau, H. Liere, Y. Lu, Y. Lubin, T. Luttermoser, B. Maas, K. Mace, F. Madeira, V. Mader, A. M. Cortesero, L. Marini, E. Martinez, H. M. Martinson, P. Menozzi, M. G. E. Mitchell, T. Miyashita, G. A. R. Molina, M. A. Molina-Montenegro, M. E. O'Neal, I. Opatovsky, S. Ortiz-Martinez, M. Nash, Ö. Östman, A. Ouin, D. Pak, D. Paredes, S. Parsa, H. Parry, R. Perez-Alvarez, D. J. Perović, J. A. Peterson, S. Petit, S. M. Philpott, M. Plantegenest, M. Plečáš, T. Pluess, X. Pons, S. G. Potts, R. F. Pywell, D. W. Ragsdale, T. A. Rand, L. Raymond, B. Ricci, C. Sargent, J.-P. Sarthou, J. Saulais, J. Schäckermann, N. P. Schmidt, G. Schneider, C. Schüepp, F. S. Sivakoff, H. G. Smith, K. Stack Whitney, S. Stutz, Z. Szendrei, M. B. Takada, H. Taki, G. Tamburini, L. J. Thomson, Y. Tricault, N. Tsafack, M. Tschumi, M. Valantin-Morison, M. Van Trinh, W. van der Werf, K. T. Vierling, B. P. Werling, J. B. Wickens, V. J. Wickens, B. A. Woodcock, K. Wyckhuys, H. Xiao, M. Yasuda, A. Yoshioka, and Y. Zou. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences* 115:E7863–E7870.
- Khodaverdi, H., T. Fowles, E. Bick, and C. Nansen. 2016. Does drought increase the risk of insects developing behavioral resistance to systemic insecticides? *Journal of Economic Entomology* 109:2027–2031.

- Kistner-Thomas, E. J. 2019. The potential global distribution and voltinism of the Japanese beetle (Coleoptera: Scarabaeidae) under current and future climates. *Journal of Insect Science* 19:16.
- Klein, A.-M., I. Steffan-Dewenter, and T. Tscharnkte. 2003. Bee pollination and fruit set of *Coffea arabica* and *C. canephora* (Rubiaceae). *American Journal of Botany* 90:153–157.
- van Klink, R., D. E. Bowler, K. B. Gongalsky, M. Shen, S. R. Swengel, and J. M. Chase. 2024. Disproportionate declines of formerly abundant species underlie insect loss. *Nature* 628:359–364.
- Kogan, M. 1998. Integrated Pest Management: Historical Perspectives and Contemporary Developments. *Annual Review of Entomology* 43:243–270.
- Kremen, C., and A. M. Merenlender. 2018. Landscapes that work for biodiversity and people. *Science* 362:eaau6020.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45:175–201.
- Lehmann, P., T. Ammunét, M. Barton, A. Battisti, S. Eigenbrode, J. Jepsen, G. Kalinkat, S. Neuvonen, P. Niemelä, J. Terblanche, B. Økland, and C. Björkman. 2020. Complex responses of global insect pests to climate warming. *Frontiers in Ecology and the Environment* 18:141–150.
- Lessio, F., C. Pisa, L. Picciau, M. Ciampitti, B. Cavagna, and A. Alma. 2021. An immunomarking method to investigate the flight distance of the Japanese beetle. *Entomologia Generalis* 42.
- Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73:1943–1967.
- Liere, H., T. N. Kim, B. P. Werling, T. D. Meehan, D. A. Landis, and C. Gratton. 2015. Trophic cascades in agricultural landscapes: indirect effects of landscape composition on crop yield. *Ecological Applications* 25:652–661.
- Lundin. 2021. Integrated pest and pollinator management – expanding the concept. *Frontiers in Ecology and the Environment*.
- MacDonald, Z. G., J. H. Acorn, J. Zhang, and S. E. Nielsen. 2019. Perceptual Range, Targeting Ability, and Visual Habitat Detection by Greater Fritillary Butterflies *Speyeria cybele* (Lepidoptera: Nymphalidae) and *Speyeria atlantis*. *Journal of Insect Science* 19:1.
- Martínez-Sastre, R., D. García, M. Miñarro, and B. Martín-López. 2020. Farmers' perceptions and knowledge of natural enemies as providers of biological control in cider apple orchards. *Journal of Environmental Management* 266:110589.

- Meehan, T. D., B. P. Werling, D. A. Landis, and C. Gratton. 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proceedings of the National Academy of Sciences* 108:11500–11505.
- Mitchell, M. G. E., E. M. Bennett, and A. Gonzalez. 2014. Agricultural landscape structure affects arthropod diversity and arthropod-derived ecosystem services. *Agriculture, Ecosystems & Environment* 192:144–151.
- Paini, D. R., A. W. Sheppard, D. C. Cook, P. J. De Barro, S. P. Worner, and M. B. Thomas. 2016. Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences* 113:7575–7579.
- Pereira, P., M. Inacio, D. Barcelo, and W. Zhao. 2025. Impacts of agriculture intensification on biodiversity loss, climate change and ecosystem services. *Current Opinion in Environmental Science & Health* 46:100637.
- Potter, D. A., and D. W. Held. 2002. Biology and management of the Japanese beetle. *Annual Review of Entomology* 47:175–205.
- Potter, M. F., D. A. Potter, and L. H. Townsend. 2006. Japanese Beetles in the Urban Landscape. <https://entomology.mgcafe.uky.edu/ef451>.
- Poveda, K., D. S. Karp, R. Chaplin-Kramer, M. Centrella, T. Luttermoser, R. Perez-Alvarez, M. E. O'Rourke, E. A. Martin, and H. Grab. 2025. The Importance of Landscape Composition for Pest Control and Crop Yield: A Global Quantitative Synthesis. *Ecology Letters* 28:e70250.
- Prakash, A., J. Rao, A. K. Mukherjee, J. Berliner, S. S. Pokhare, T. Adak, S. Munda, P. R. Shashank, Applied Zoologists Research Association, and Central Rice Research Institute (India). 2014. Climate change: impact on crop pests. Applied Zoologists Research Association (AZRA), Central Rice Research Institute, Cuttack, Odisha, India.
- Roy, H. E., A. Pauchard, P. Stoett, T. Renard Truong, S. Bacher, B. S. Galil, P. E. Hulme, T. Ikeda, K. Sankaran, M. A. McGeoch, L. A. Meyerson, M. A. Nuñez, A. Ordonez, S. J. Rahlao, E. Schwindt, H. Seebens, A. W. Sheppard, and V. Vandvik. 2024. IPBES Invasive Alien Species Assessment: Summary for Policymakers. Zenodo.
- Rusch, A., R. Chaplin-Kramer, M. M. Gardiner, V. Hawro, J. Holland, D. Landis, C. Thies, T. Tscharntke, W. W. Weisser, C. Winqvist, M. Woltz, and R. Bommarco. 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. *Agriculture, Ecosystems & Environment* 221:198–204.
- Sánchez-Bayo, F., and K. A. G. Wyckhuys. 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation* 232:8–27.
- Shanovich, H. N., A. N. Dean, R. L. Koch, and E. W. Hodgson. 2019. Biology and management of Japanese beetle (Coleoptera: Scarabaeidae) in corn and soybean. *Journal of Integrated Pest Management* 10:9.

- Skendžić, S., M. Zovko, I. P. Živković, V. Lešić, and D. Lemić. 2021. The impact of climate change on agricultural insect pests. *Insects* 12:440.
- Steffan-Dewenter, I., U. Münzenberg, C. Bürger, C. Thies, and T. Tscharntke. 2002. Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. *Ecology* 83:1421–1432.
- Steffan-Dewenter, I., and T. Tscharntke. 1997. Early succession of butterfly and plant communities on set-aside fields. *Oecologia* 109:294–302.
- Tamburini, G., G. Santoiemma, M. E. O'Rourke, R. Bommarco, R. Chaplin-Kramer, M. Dainese, D. S. Karp, T. N. Kim, E. A. Martin, M. Petersen, and L. Marini. 2020. Species traits elucidate crop pest response to landscape composition: a global analysis. *Proceedings of the Royal Society B: Biological Sciences* 287:20202116.
- Teixeira, P. L. P., F. A. Spagnuolo, J. M. Ferreira, and T. S. Telles. 2025. Perception and knowledge of organic farmers about pests and natural enemies. *Brazilian Journal of Biology = Revista Brasileira De Biologia* 85:e293825.
- Thies, C., and T. Tscharntke. 1999. Landscape structure and biological control in agroecosystems. *Science (New York, N.Y.)* 285:893–895.
- Thomson, L. J., S. Macfadyen, and A. A. Hoffmann. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control* 52:296–306.
- Thurman, J. H., D. W. Crowder, and T. D. Northfield. 2017. Biological control agents in the Anthropocene: current risks and future options. *Current Opinion in Insect Science* 23:59–64.
- Tscharntke, T., A. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874. *Ecology Letters* 8:857–874.
- Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, R. M. Ewers, J. Fründ, R. D. Holt, A. Holzschuh, A. M. Klein, D. Kleijn, C. Kremen, D. A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W. H. van der Putten, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews of the Cambridge Philosophical Society* 87:661–685.
- Urbaneja-Bernat, P., V. Ibáñez-Gual, M. Montserrat, E. Aguilar-Fenollosa, and J. A. Jaques. 2019. Can interactions among predators alter the natural regulation of an herbivore in a climate change scenario? The case of *Tetranychus urticae* and its predators in citrus. *Journal of Pest Science* 92:1149–1164.
- Veres, A., S. Petit, C. Conord, and C. Lavigne. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems & Environment* 166:110–117.

- Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences* 118:e2023989118.
- Wen, Z., Y. Fu, H. Zheng, and Z. Ouyang. 2024. Metapopulation networks unlock the effects of landscape fragmentation on agricultural pests and natural predators. *Global Ecology and Conservation* 50:e02849.
- Wiens, J. A. 1989. Spatial Scaling in Ecology. *Functional Ecology* 3:385–397.
- Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes*. *Landscape Ecology*. Vol. 15 p. 523-533. (2000) 15.

Chapter 2 - Precipitation moderates the effects of surrounding landscape composition on insect communities

Submitted as: Kucherov N.B. & Kim T.N. Precipitation moderates the effects of surrounding landscape composition on insect communities.

Abstract

Semi-natural land cover in agroecosystems can support populations of insect natural enemies and pollinators, through resources such as nesting sites, alternative nutritional resources, and overwintering sites. Some studies support that increasing amounts of semi-natural lands near agricultural fields could increase the abundance of natural predator insects and pollinating insects and decrease the number of pest insects within the fields. However, meta-analysis across large spatial extents and multiple years show inconsistent results, with semi-natural lands having both positive and negative effects on natural predators and pests. This could be due to interactions between climate and landscape variables. Currently, research on the combined or interactive effects of landscape and seasonal climate variables on agricultural pests or predators is lacking. In this research, we systematically evaluate the effects of semi-natural land cover within the surrounding landscape, precipitation, and bordering edge types on insect abundance and community composition within one consistent study design using sites along a strong semi-natural-agricultural gradient. Model comparisons indicate that an interaction between surrounding semi-natural land and precipitation better explained pollinator and predator abundance, while pest abundance was best explained by the combined effects. Abundance also varied significantly across field locations for pests and predators. Variation in pest and predator communities was driven primarily by climatic factors, while pollinator community variation was mainly driven by the proportion of semi-natural land. Our study provides evidence of significant interactions between seasonal precipitation and land cover, where precipitation can mask or minimize the effects of land cover on insect populations at lower precipitation levels.

Introduction

Agricultural systems today face the pressing challenge of maintaining high levels of crop productivity while conserving biodiversity, and sustainable pest management is a key issue (Pretty 2018; Petit et al. 2020). From a landscape ecology perspective, agricultural fields are habitat patches embedded within a broader landscape matrix composed of diverse elements such as hedgerows, pastures, other crops, and roadsides. This broader landscape matrix influences the animal and plant communities and ecosystem services within agricultural fields (Zhang et al. 2007) through species exchange (Leibold et al. 2004) and resource supplementation (Tscharntke et al. 2005). The preservation of semi-natural land within agricultural landscapes may be helpful for pest management through its support for natural enemies, which often rely on non-crop habitats for nesting sites (Klaus et al. 2021), alternative foraging resources (Cohen et al. 2023; Magagnoli et al. 2024), and overwintering sites (Clem and Harmon-Threatt 2021; Bannwart et al. 2025). There is support for the concept that agricultural fields within landscapes which are more structurally diverse have higher natural enemy biodiversity (Tscharntke et al. 2005), increased pollinator abundance (Holzschuh et al. 2013; Carrié et al. 2018) and improved suppression of pest species by natural enemies (Gurr et al. 2017) because neighboring non-crop habitats can facilitate the colonization of crop fields by beneficial insects (Landis et al. 2000; Gurr et al. 2017; Biegerl et al. 2025). However, pest species may also benefit from the resources of surrounding semi-natural land (Carsten Thies et al. 2005; Martin et al. 2013; John M Holland et al. 2016; Akter et al. 2023) and increases in natural enemy abundance may not be able to adequately suppress certain pest populations (Ragone et al. 2025).

While some studies have found semi-natural areas supporting beneficial insect populations, we do not always consistently see the expected results of increased beneficial insects and fewer pests within the agricultural fields (Veres et al. 2013; Tscharntke et al. 2016; Karp et al. 2018). Veres et al. (2013) found that fields within landscapes with higher proportions of semi-natural areas had lower pest abundance or higher pest control in only 45 out of 72 independent case studies. An extensive global meta-analysis by Karp et al. (2018) of 6,759 sites across 31 countries found that semi-natural areas and agricultural areas in the surrounding landscape had inconsistent effects on pest and predator abundance and predation rates. These inconsistent results could arise because species traits, such as exotic status, host plants, and habitat breadth, can influence how crop pest insects respond to semi-natural land cover in the surrounding landscape (Tamburini et al. 2020). However, inconsistent results may also stem from the differences across the studies themselves, such as sampling locations (edges v. interiors) or geographical and temporal variation in local climate variables. Thus, significant effects of landscape composition could be present across these studies but masked by other variables such as climate and farm management practices.

In addition to landscape and local habitat factors, climate plays a large role in the abundance and richness of insects in agricultural fields. For example, a warmer climate leads to higher insect abundances (Altermatt 2009) and higher crop losses from insect pests (Deutsch et al. 2018). Temperature and rainfall may be the most important variables when considering crop-insect interactions as higher temperatures increase the number of reproductive generations and higher precipitation reduces thermo-hydro stress (Ma et al. 2025). Therefore, warmer landscapes may experience more spillover from semi-natural areas into agricultural fields due to the overall higher abundance of insects. Additionally, drought can reduce populations of beneficial insects,

spiders, and birds (Rosenzweig et al. 2001), and dry conditions may override any beneficial effects from semi-natural land cover within the landscape.

While the effects of interactions between climate and landscape variables on broad biodiversity patterns are increasingly recognized (Guo et al. 2018; Peters et al. 2019; Nunez and Alkemade 2021), few studies look at the combined or interactive effects of climatic and landscape variables on agricultural pests or predation (Fricke et al. 2022; Courson et al. 2022). In a recent study on the relative effects of landscape and seasonal weather on pest variation across different regions of France, Courson et al. (2022) found that regional proportions of grassland had a consistently negative effect on the presence of insect pests while seasonal weather variables were an important factor in inter-regional differences. Fricke et al. (2022) looked at the interactive effects of landscape, microclimate (on-site temperature and humidity during caterpillar exposure), and long-term climate (30 year mean annual temperature) on arthropod predation rates. They found that predation rates were affected by microclimate (less predation in low temperatures and high humidity), and landscape composition (increased predation with increasing land cover diversity), but found no interactive effects of landscape and climate (microclimate or long-term climate). It is possible that seasonal climate factors are more important to pest and predator population dynamics (Courson et al. 2022) than microclimate or long-term climate factors. Interactive effects of landscape and seasonal climate could possibly mask significant landscape effects and therefore need to be considered.

Previous meta-analyses of in-field insect populations found that although natural enemy populations were often positively affected by surrounding semi-natural areas in the landscape (Bianchi et al. 2006; Chaplin-Kramer et al. 2011), the biodiversity and abundance of natural predators varied depending on location within a field (Boetzel et al. 2024). Semi-natural edges

had a positive effect on the abundance of insect predators and pollinators in many studies (J. M. Holland et al. 2012; González et al. 2016; Samaranayake and Costamagna 2018; Boetzl et al. 2024) but often decreased with increasing distance towards field centers (González et al. 2016; Boetzl et al. 2024). Edges are therefore likely to support different species than field interiors because insects from the field borders spill over to the edges and stay there (Ries et al. 2004; Rand et al. 2006; Boetzl et al. 2024; Harman and Kim 2024). Insects can be encouraged to move from edges into fields by complementary resource use and species interactions (Ries et al. 2004; Rand et al. 2006), and their movement usually tracks temporal resources such as prey and nectar (Knapp and Řezáč 2015; Iuliano and Gratton 2020; Gomez Villegas et al. 2025)

Understanding the conditions under which beneficial effects of landscape composition are masked by other variables is essential for developing effective, ecologically sound strategies for improving pest management (N. A. Schellhorn et al. 2014; Nancy A. Schellhorn et al. 2015) and pollination (Biegerl et al. 2025). Here, we systematically evaluate the effects of semi-natural land cover within the surrounding landscape, precipitation, and bordering edge types on insect abundance and community composition within one consistent study design. We have the following hypotheses: (i) surrounding semi-natural area will affect the insect community at a landscape level, providing nesting area for pollinators and predators, and acting as a source of beneficial insects; (ii) precipitation will have a positive effect on insect abundance across the sites and years; (iii) analyzing the interaction between landscape and precipitation will show that low precipitation suppresses the effect of semi-natural surrounding areas on insect abundance; (iv) bordering fields will have varying effects on the nearby edge of the field of interest, which will not extend fully into the center of the field and the interaction between landscape and local edge type may amplify the effect of semi-natural surrounding areas; (v) insect community

composition will change in response to landscape variation with different species dominating communities in fields surrounded by more agriculture compared to fields surrounded by more semi-natural area. By clarifying interactions between landscape and climate variables and additive effects of local variables, we will be able to tease apart possible benefits of semi-natural land cover from the effects of seasonal precipitation and make relevant recommendations for the restoration of natural areas within agricultural landscapes.

Methods

Study Region

This study was replicated across 61 sites in eastern Kansas during the summers of 2023 and 2024. Kansas has a very pronounced annual precipitation gradient which spans the state and varies from under 400 mm in the southwest to over 1200 mm in the southeast (Figure 1). With Kansas' unique precipitation gradient, we can examine interactions between semi-natural lands and precipitation to determine how climatic differences may affect the benefits of semi-natural land. The regional norm for cropping systems in this area is a corn–soybean rotation with pesticides applied as needed and a predominance of no-till practice. Because the fields are close in space, within the same region, and managed by farmers with similar culture and practices, this allows us to focus on gradients within the precipitation and semi-natural land variables while other variables stay relatively constant.

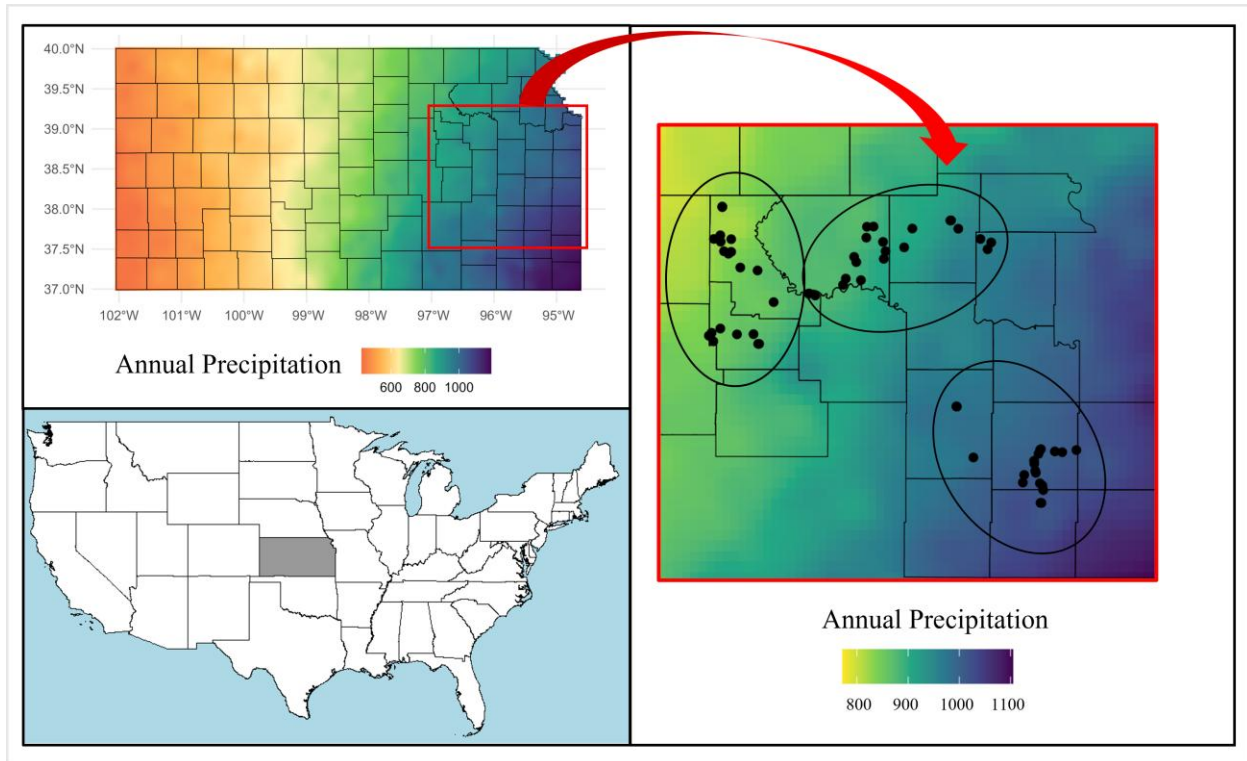


Figure 2-1 Map of the 30-year normal annual precipitation ranges across Kansas (top left) which is located in the central United States (bottom left), and 30-year normal annual precipitation ranges across our study area with study sites represented by black dots and ecoregions indicated with black circles (right). Precipitation values were derived from the Prism 30-year normal precipitation raster.

Kansas is located in the center of the United States, in the Northern Plains region. Land use in the Northern Plains is dominated by cropland (51%), followed by grassland and pasture (41%) (Winters-Michaud 2024). Soybean (*Glycine max*) is the second most planted crop in the United States by acreage, with 83.4 million acres planted in 2025 (National Agricultural Statistics Service 2025) and generating \$124 billion annually (Checkoff 2023). It is a close second to corn (*Zea mays*), of which 95.2 million acres were planted in 2025, and nearly double the acreage for wheat (*Triticum aestivum*) which covered 45.5 million acres in 2025 (National Agricultural Statistics Service 2025). The Northern Great Plains temperate grassland ecosystem is one of the most endangered and least protected ecosystems on earth, and factors such as land

conversion have led to a loss of 62% of North American temperate grasslands (Monnett and Stone 2025). Most of this land is privately owned, therefore establishing common priorities and principles across community stakeholders is vital for the preservation of this ecosystem and the ecosystem services it provides. Northeast Kansas has one of the largest areas of remaining tallgrass prairie, enabling us to examine a very broad gradient of semi-natural areas around our sites (3% to 92%).

Site selection

To select our sites, we worked with soybean growers in our community who allowed us access to over 100 fields. During site selection, we considered only sites planted with full season, indeterminate soybeans. Sites were chosen to fall along a gradient of surrounding semi-natural area at a 2 km radius (Figure 2). The percentage of semi-natural areas in the 2 km surrounding the sites ranged from 3% to 92% (Figure 2). In 2022, there was a minimum distance of 4 km between sites (mean = 8.5 km, max = 24 km). In 2023, we had to adjust our minimum distance to 2 km between sites because some of our collaborators had their soybean fields planted much closer together due to planting rotations (mean = 4 km, max = 42 km). Each year, 30 sites were sampled, with an additional site sampled in the first year.

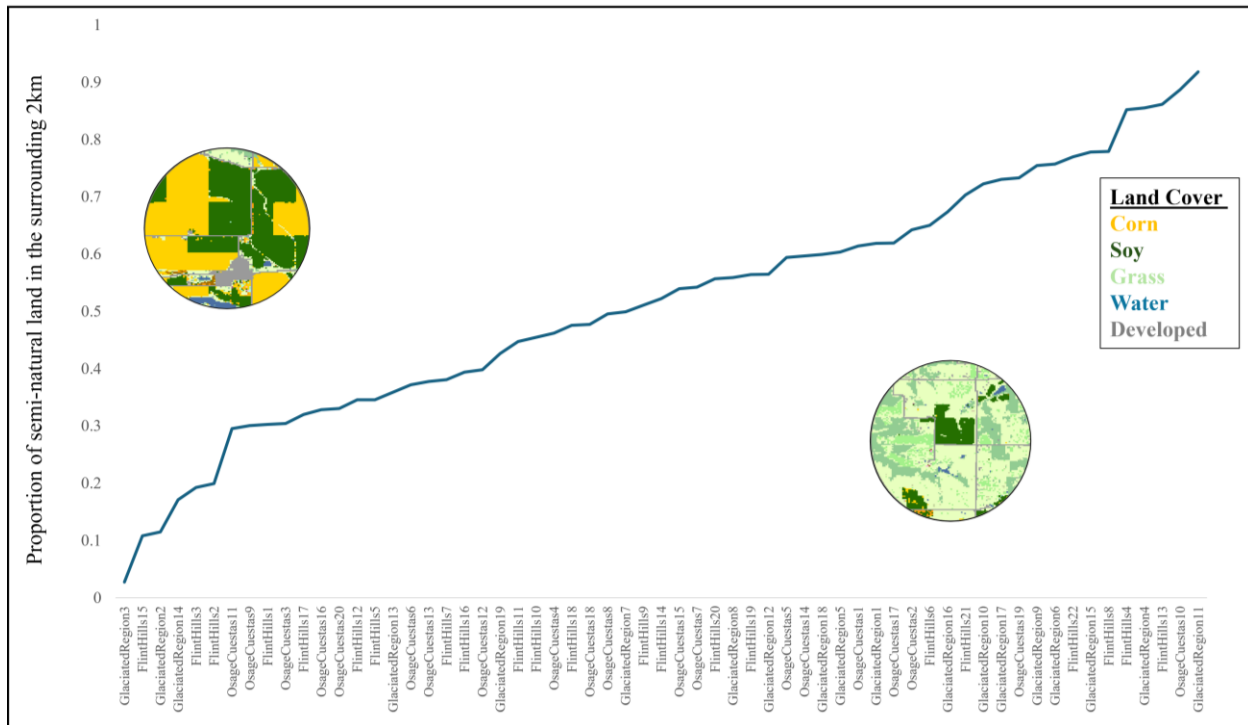


Figure 2-2 Percentage of surrounding semi-natural area within a 2-kilometer radius for each field within the study. Semi-natural area included areas identified as grassland, pasture, forest, or wetland in USDA’s annual Cropscape raster for the corresponding study year.

Sites fell within three physiographic ecoregions: the Flint Hills uplands, the Glaciated Region, and the Osage Cuestas, determined mainly by differences in physical geology, but also slight differences in climate (Kansas Geological Survey 2025). The Flint Hills ecoregion was formed by the erosion of limestone of an inland sea and is characterized by clay soil containing flint and a lack of trees (Kansas Geological Survey 2025). The Glaciated Region was invaded by at least two glaciers and is characterized by soils left behind from glacial drift which include thick layers of silt (Kansas Geological Survey 2025). The Osage Cuestas are characterized by steep cliffs with a gentle slope on one side called cuestas, flood plains, and rolling hills with soil that is a mixture of clay, silt, and limestone (Kansas Geological Survey 2025). All sites within this study were located within the land cover historically identified as Tallgrass Prairie at the

time of European settlement in Kansas (Kansas Native Plant Society 2021). It is possible that these regional differences could influence local insect communities. To separate the influence of surrounding semi-natural areas from possible regional effects, sites were chosen to fit the full gradient for surrounding semi-natural areas within each physiographic ecoregion.

Insect community sampling and abundance calculations:

For sampling, sweeps were conducted along a 50 meter transect (approximately 100 sweeps of the net) at a constant, moderate pace in the interior of the field, as well as on the edges of the field. An effort was made to reach the true center of the field. However, for fields that were over 100 acres, interior sweeps were made at least 200 meters into the field. For edge sampling, five sites with a semi-natural edge (either semi-natural grassland, pasture or a creek edge) and five sites with an agricultural edge were sampled within each region. If plants were flowering, an additional targeted vacuum sampling was performed along the 50-meter transect for a timed period of 10 minutes. Sampling did not occur if it was raining, wind speeds were above 2.5 m/s (Brittain et al. 2013; Balfour and Ratnieks 2025), or a farmer had recently sprayed the field with pesticides. In 2023, sites were sampled three times; once during the initial growth period of the soybeans (24 June – 13 July), once during the reproductive stage of flowering (11 July – 2 August), and once while the soybean plants had pods (15 August – 1 September). Due to logistical issues (i.e., late season spraying, weather) each site was sampled twice in 2024, once during the initial growth period of the soybeans, and once during the reproductive stage of flowering.

Samples were put on ice in a cooler during the day of field work, then transferred to a freezer (-18 °C) until the samples could be processed. For identification, all insects were removed from the bag and leaves and placed into petri dishes for identification underneath a dissecting microscope. Well-known pests of concern were identified to species (e.g. bean leaf beetle (*Cerotoma trifurcate*) or Japanese beetle (*Popillia japonica* Newman)) or grouped together into functional groups at higher taxonomic levels, for example stinkbugs were identified to family Pentatomidae, except for the predatory stink bug, *Podisus maculiventris*, which was identified to species. Other insects were grouped by higher taxa, such as family e.g. Cicadellidae (leafhoppers) and Cercopidae (froghoppers), Reduviidae (assassin bugs) and Nabidae (damselflies), and Coccinellidae (lady beetles) or order, e.g. Hymenoptera, depending on the ecosystem functions performed within the groups.

Abundance of pests, predators, and pollinators were summed across sampling rounds by transect (Appendix A, Table A.1) but due to differences in sampling effort (three rounds in 2023 and two rounds in 2024), the mean insect abundance per transect was calculated. Thrips (Thysanoptera) and whiteflies (Aleyrodidae) were excluded from the pest calculations as their numbers varied greatly based on how many leaves were in the sweep, and they occurred in such higher numbers than the other pests that it would obscure overall abundance trends. Pollinators included all species of bees as well as hoverflies. Lepidoptera were generally moths or butterflies whose larvae are pests of soybean, and as such were included in the pest category.

Seasonal climate data

For climate and landscape analyses, we utilized R and packages including tidyverse (Wickham et al. 2019), tigris (Walker 2016), raster (Hijmans, Etten, et al. 2025), sf (Pebesma

2018; Pebesma and Bivand 2023), and terra (Hijmans, Barbosa, et al. 2025). Weather data was collected using the PRISM weather data in R using the package prism (Hart and Bell 2015). Our climate variables, seasonal precipitation and summer maximum temperature, were chosen for their relevancy to the biological processes of insect communities. Precipitation and temperature are fundamental drivers of insect ecology, influencing development rates, survival, dispersal, and community interactions. We calculated seasonal precipitation as the sum of precipitation from the PRISM monthly precipitation rasters for May, June, July, and August to capture influential periods for spring host plant and insect development as well as precipitation during our study period, while avoiding portions of annual precipitation that come from winter snowfall or occur after our study ends. Seasonal precipitation reflects water availability and vegetation productivity across the growing season, and affects factors such as floral resources, host plant quality, and microhabitat humidity which strongly shape pollinator and herbivore populations (Beirne 1970). Summer maximum temperature captures thermal conditions that regulate insect metabolic rates and phenology (González-Tokman et al. 2020). Higher maximum temperatures can accelerate pest development and generation turnover (Pareek et al. 2017), but may also limit insects' ability to thermoregulate, reducing survival and foraging efficiency (Harvey et al. 2020). We calculated summer maximum temperature by taking the mean of PRISM monthly maximum temperature rasters from the months of June, July, and August in order to capture the maximum temperatures across the warmest months, and the entire time of our study period.

Landscape analysis

The proportion of surrounding semi-natural land and grassland were calculated separately at 500 m, 1 km, 1.5 km, and 2 km using CropScapeR (Chen 2020), cdlTools (Lisic et al. 2024),

and foreach (Daniel et al. 2022). To estimate semi-natural land cover, we aggregated land-cover classes including deciduous forest, coniferous forest, mixed forest, shrubland, herbaceous grassland, wetlands, and hay/pasture, following Thies et al. (2003) and Thies & Tschamtkke (1999). We then calculated the percentage of this combined ‘semi-natural land’ category within various buffers around each site. As the main semi-natural land cover in this area is grassland, we created two sets of model option; one including all semi-natural land covers (forests, wildflowers, grassland and pasture, shrublands, wetlands, and non-alfalfa hay), and one specifically for grassland (grassland, pasture, and non-alfalfa hay).

Previous studies have shown that the scale at which surrounding semi-natural area effects abundance can vary by insect group (Carsten Thies et al. 2003), so we compared the R-squared values of surrounding semi-natural land models ($y \sim$ proportion of semi-natural land) and surrounding grassland models ($y \sim$ proportion of grassland) across buffer radii of 500m, 1000m, 1500m, and 2000m separately for pests, predators, and pollinators to determine which radius was most suitable for each group. Grassland at a radius of 1 km was found to be most suitable for pests indicated by the highest R² value ($R^2 = 0.09$, other radii for grassland and semi-natural had R² values ranging 0.025 – 0.076) and for predators indicated by the highest R² value ($R^2 = 0.072$, other radii for grassland and semi-natural had R² values ranging 0.022 – 0.067). For pollinators, R² values indicated that semi-natural land at the 2 km radius would be most suitable ($R^2 = 0.062$, other radii for grassland and semi-natural had R² values ranging 0.022 – 0.067). This is consistent with scales used in previous studies which have commonly used a 1 km radius for predators or pest suppression (Carsten Thies et al. 2005; Rusch et al. 2016; Bosem Baillod et al. 2017; Lavandero et al. 2025) and a 2 km radius for pollinators (Kremen et al. 2004; Ekroos et al. 2013; Pardee et al. 2023; Vega et al. 2023).

Statistical analysis

We used generalized linear mixed-effects models (GLMMs) with a log link function to identify the individual effects of proportion of semi-natural land, seasonal weather (seasonal precipitation, summer maximum temperature), and local edge type on insect pests, predators, and pollinators. The full models for all three groups included the semi-natural land variable as identified in our landscape analysis, local edge type identified as the transect location (agricultural edge, semi-natural edge, road edge, or field center), the ecoregion within which the site is located (Flint Hill, Osage Cuestas, Glaciated Region), and the year (2023, 2024). Because three transects were surveyed within a site, SiteID, a combination of the site's name and year, was included as a random variable.

Variance inflation factors were calculated using the vif function in the package car. As our model includes both continuous and categorical variables, we also assessed Generalized VIF (GVIF) which adjusts for the varying degrees of freedom between variables (John Fox and Monette 1992). Of our fixed effects, year had the highest GVIF of 2.9, suggesting correlation with the next highest variable, seasonal precipitation. Once year was removed, all variables had a GVIF <2. A GVIF between 2-3 suggest moderate correlation (John Fox 2015), so we compared models with and without the year variable. Finding no significant difference between the models, we removed year as a variable to avoid correlation issues. GVIF scores did not indicate a correlation between ecoregion (1.06) and seasonal precipitation (1.37) or summer maximum temperature (1.68).

Additive models were fit using the glmmTMB package in R (Brooks et al. 2017), which allows flexible specification of non-Gaussian distributions and random effects. To ensure model

stability and reduce numerical issues during model estimation, particularly in interaction models, continuous environmental predictors (e.g., land cover, precipitation and temperature) were standardized (mean = 0, SD = 1). The Tweedie distribution was used to adequately capture the distributional structure and variability in mean insect abundance across sites, with characteristics including continuous, strictly positive, right-skewed data which contained zeros. Model fit was assessed using residual diagnostics from the DHARMA package (Hartig 2025), including tests for overdispersion, residual uniformity, and zero-inflation. Diagnostics indicated a good fit and no overdispersion for pests (dispersion = 1.099, $p = 0.584$; Kolmogorov–Smirnov $D = 0.058$, $p = 0.604$; zero-inflation $p = 1$), predators (dispersion = 1.099, $p = 0.48$; Kolmogorov–Smirnov $D = 0.047$, $p = 0.839$; zero-inflation $p = 0.736$), or pollinators (dispersion = 1.28, $p = 0.28$, Kolmogorov–Smirnov $D = 0.03$, $p = 0.997$; zero-inflation $p = 0.792$). Our base additive model was written as:

Equation 1: $\text{glmmTMB}(y \sim \text{land cover} + \text{seasonal precipitation} + \text{summer average maximum temperature} + \text{Ecoregion} + \text{Location} + \text{Year} + (1 \mid \text{SiteID}), \text{ data} = \text{data}, \text{ family} = \text{tweedie})$

For pest and predator abundances, the fixed effects included proportion of grass cover within 1 km, summer precipitation, and average maximum summer temperature, as well as categorical predictors including ecoregion and transect location. For pollinators, the fixed effects included the proportion of semi-natural land cover within 2 km rather than grass cover. All models included a random intercept for SiteID to account for repeated sampling within sites.

To assess possible interactions between semi-natural land cover or grass cover and our other variables, we created separate interaction models for interactions between land cover and seasonal climate (precipitation and maximum temperature), local edge type and ecoregion. The

candidate interaction models are listed in Table 1. We used Akaike's Information Criterion (AIC) to compare overall model fit among the base additive model and four candidate interaction models and assess overall model parsimony (Burnham and Anderson 2004). Because our primary goal was to test whether environmental interactions influence insect group abundance, we additionally performed likelihood ratio tests (LRTs) for nested models to evaluate whether including each interaction significantly improved model fit relative to the base additive model (Bolker et al. 2009) and infer the statistical support for specific interaction terms.

Table 2-1 Description of candidate interaction models to clearly show differences between the interaction and fixed effect variables within in each of the candidate models used to test if interactions improved model fit over the additive model.

Candidate Model Number	Interaction variables	Fixed effect variables	Random effect variable	Model type
1	land cover * seasonal precipitation	summer average maximum temperature + location + ecoregion + year	site ID	tweedie
2	land cover * summer average maximum temperature	seasonal precipitation + location + ecoregion + year	site ID	tweedie
3	land cover * location	seasonal precipitation + summer average maximum temperature + ecoregion + year	site ID	tweedie
4	land cover * ecoregion	seasonal precipitation + summer average maximum temperature + location + year	site ID	tweedie

For visualization of main effects and interactions, predicted values were generated from the scaled models and back-transformed to their original units using observed means and standard deviations, allowing interpretation in ecologically meaningful units (e.g., mm of precipitation, proportion of semi-natural land cover). Marginal predictions were computed with the `ggeffects` package (Lüdtke 2018) using `ggpredict()`, holding other continuous covariates at their mean and categorical covariates at their reference level. For precipitation interactions, standardized variables were back-transformed for plotting, and levels were labeled “Low,” “Medium,” and “High” (−1 SD, 0, +1 SD. All visualizations, created with `ggplot2` (Wickham 2016), include 95% confidence intervals and are presented on the response scale for ecological clarity.

Constrained Ordination Analysis

To examine the influence of our environmental variables on the community composition of the three main insect functional groups (pests, pollinators, and predators), we used a combination of permutational multivariate analysis of variance (PERMANOVA) and distance-based redundancy analysis (db-RDA). All analyses were conducted in R (v4.5) using the packages *vegan* (Oksanen et al. 2025), *tidyverse* (Wickham et al. 2019), *ggrepel* (Slowikowski et al. 2024) and *grid* (“R: The Grid Graphics Package” 2024). A community matrix was created for each group (pests, predators, pollinators) as a transect-site by species matrix with the average abundance across the season per transect as entries in the cells. Prior to multivariate analyses, community abundance data were transformed using the Hellinger transformation to reduce the influence of highly abundant species and to improve the suitability of the data for ordination based on Euclidean distances (Legendre and Gallagher 2001). A corresponding environmental variables matrix was constructed with site specific environmental data. Environmental variables included proportion of grassland in the surrounding 1 km, proportion of semi-natural area in the surrounding 2 km, summer average maximum temperature, summer average precipitation, ecoregion, and transect location. Prior to analysis, all numeric environmental variables were standardized and checked for multicollinearity using the package *car* (J. Fox and Weisberg 2019). No variables were highly correlated ($|r| < 0.70$), and all were retained for analyses.

Differences in community composition were tested using PERMANOVA, with the *adonis2()* function in *vegan* (Oksanen et al. 2025), based on Bray–Curtis dissimilarities and 999 permutations. Interaction terms were evaluated during model selection; however, because their inclusion did not meaningfully improve adjusted R^2 , final models included only main effects. The most parsimonious model for each insect group was selected to evaluate the effects of

environmental variables on community composition. For visualization, we ran distance-based redundancy analyses (db-RDA) using the `capscale()` function in `vegan`, with Bray–Curtis dissimilarities as the response distance measure and environmental variables as constraints. Site scores, species scores, and environmental vectors were extracted from the db-RDA results using the `scores()` function and visualized using `ggplot2`. The significance of db-RDA models and individual constrained axes was assessed using permutation tests (`anova()`, 999 permutations). Environmental vectors were fitted to ordination space using the `envfit()` function to obtain vector coordinates, coefficients of determination (r^2), and associated p-values. Environmental vectors were scaled for visualization to improve interpretability, without altering their statistical meaning.

Results

Across the 61 sites in this study, 108,626 arthropods were identified from 420 sweep and 241 vacuum samples (List in Appendix A: Table A.1). The average number of arthropods in a transect was 259, with a median of 197, a minimum of 5, and a maximum of 2135. High variation in transect counts was mainly due to large numbers of thrips (25,964) and whiteflies (34,152) which correlated with the number of leaves caught in the sweep and were therefore not included in the analysis. In total, 14,915 insects were identified as key pests (14%) while 12,547 insects and spiders were identified as predators (12%). The abundance of bees and hoverflies identified as pollinators was 547 (<1%). The three most abundant pest insects were leaf and frog hoppers (3275, 22% of pests), bean leaf beetles (2176, 15% of pests) and Japanese beetles (1464, 10% of pests). The three most abundant predators were spiders (5655, 45% of predators), parasitic wasps (2299, 18% of predators) and minute pirate bugs (2270, 18%). Honey bees were

the most abundant pollinators (226, 41% of pollinators) followed by sweat bees (162, 30% of pollinators), and hover flies (65, 12% of pollinators).

Landcover and climate effects on pest abundance and community composition

For pest abundance, the percent grass * precipitation interaction model (candidate model 1, Table 1) showed a marginally significant improvement over the base additive model ($\chi^2 = 3.11$, $df = 1$, $p = 0.078$; $\Delta AIC = -1.11$), while other interaction models with location, ecoregion, or temperature interactions (candidate models 2, 3, and 4) did not improve model fit ($p \geq 0.159$; ΔAIC range = $+0.82$ to $+3.74$), indicating that the additive model was the most parsimonious. Given the weak statistical support for the interaction, we retained the additive model for primary inference but included the interactive model results for reference (Appendix A, Table A.2). Our best supported model (base additive model) showed that the proportion of grassland in the surrounding 1 km landscape had a negative effect on pests (Estimate -0.196 ± 0.073 SE, $p < 0.01$, Table 2, Figure 3), while the effect of seasonal precipitation was not significant ($p = 0.17$).

Table 2-2 Results from the most parsimonious additive or interaction generalized linear mixed-effects models evaluating the effects of semi-natural land cover (proportion grassland or total semi-natural land), seasonal precipitation, ecoregion (Glaciated or Cuestas relative to Flint Hills), local edge type (agricultural, road, or semi-natural), and summer maximum temperature on (1) pest abundance, (2) predator abundance, and (3) pollinator abundance. All fixed-effect predictors included in the full models are shown; the random effect of site is not displayed. Significant effects are identified in bold font. Effects of categorical variables are shown as model coefficients relative to the reference level (field center for location, and Flint Hills for ecoregion). The overall effect of ecoregion was evaluated using likelihood ratio tests and Tukey-adjusted post-hoc comparisons (see Results).

Variable	Pest estimate- additive model	Predator estimate – interaction model	Pollinator estimate – interaction model
Land cover * precipitation interaction	<i>NA</i>	-0.099 ± 0.049 (p < 0.05)	0.196 ± 0.094 (p < 0.05)
Grass or semi-natural land cover	-0.196 ± 0.073 (p < 0.01)	-0.168 ± 0.057 (p < 0.01)	0.307 ± 0.104 (p < 0.01)
Seasonal Precipitation	-0.115 ± 0.084 (p = 0.17)	0.128 ± 0.066 (p = 0.05)	-0.144 ± 0.135 (p = 0.282)
Summer Average Maximum Temperature	-0.002 ± 0.103 (p = 0.99)	-0.004 ± 0.094 (p = 0.96)	0.129 ± 0.147 (p = 0.38)
Agricultural Edge	0.497 ± 0.110 (p < 0.001)	0.412 ± 0.097 (p < 0.001)	-0.238 ± 0.164 (p = 0.15)
Road Edge	0.324 ± 0.092 (p < 0.001)	0.145 ± 0.087 (p = 0.09)	0.266 ± 0.121 (p < 0.05)
Semi-Natural Edge	0.236 ± 0.119 (p < 0.05)	0.285 ± 0.106 (p < 0.01)	-0.075 ± 0.167 (p = 0.65)
Osage Cuestas	0.137 ± 0.149	0.042 ± 0.114	-0.307 ± 0.229
Glaciated Region	0.348 ± 0.167	-0.028 ± 0.127	-0.121 ± 0.249

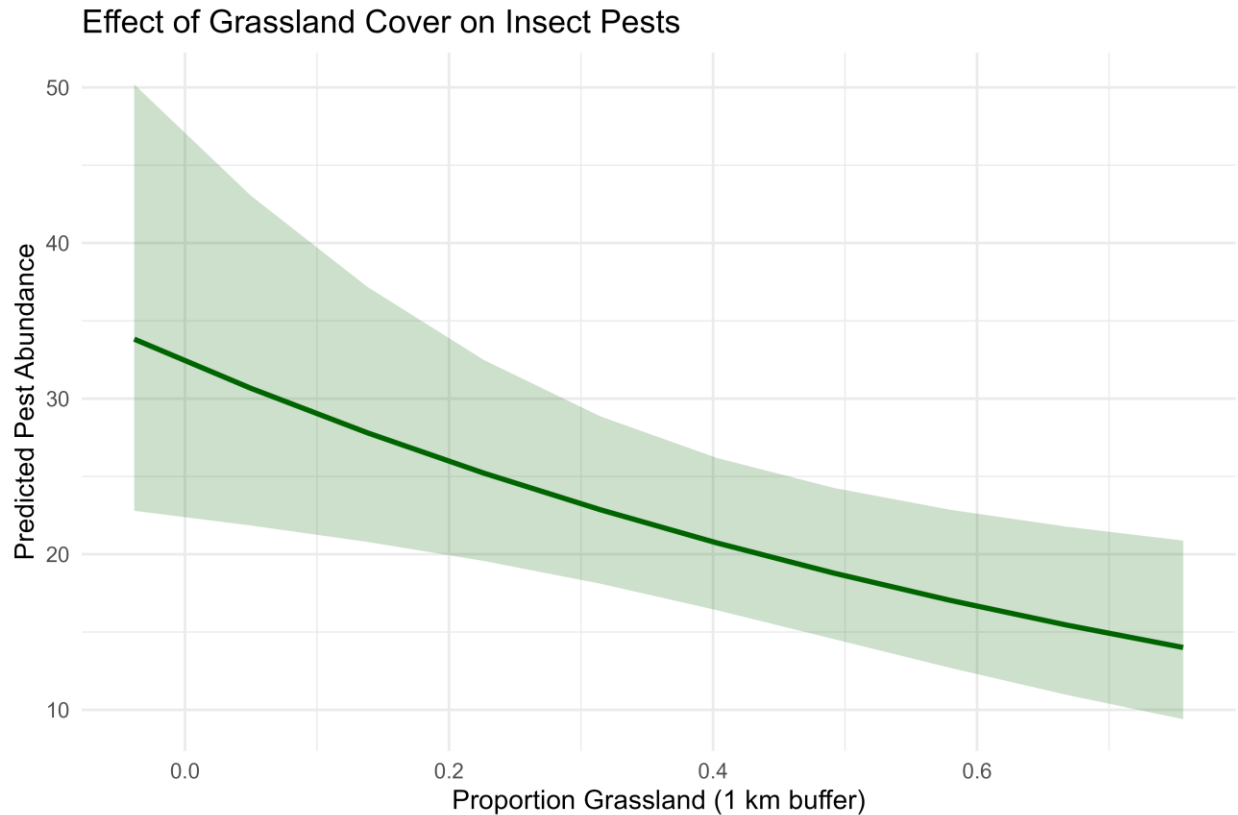


Figure 2-3 Effect of surrounding grassland cover on insect pest abundance, with grassland shown on its original scale as the proportion of grassland within a 1-km buffer. The solid line represents the model predictions, while the shading indicates 95% confidence intervals. Predictions are presented on the response scale, with all other covariates held at their mean values.

Contrastingly, pest community composition was influenced by climatic variables as well as landcover. PERMANOVA results indicated that community composition was significantly associated with seasonal precipitation ($R^2 = 0.017$, $p < 0.01$), summer average maximum temperature ($R^2 = 0.013$, $p < 0.01$), and the proportion of grassland within 1 km ($R^2 = 0.011$, $p < 0.01$). The db-RDA shows that environmental variables collectively explained a significant portion of variation in pest community composition communities ($R^2 = 0.165$, $F_{8,167} = 4.13$, $p = 0.001$), while variation was spread across four constrained axes (CAP1–CAP4, $p < 0.01$), suggesting that pest community differences are structured by multiple combinations of

environmental and spatial variables. Climatic factors were strong drivers of community variation, with seasonal precipitation having stronger effects on communities dominated by detritus stem borers and grasshoppers/crickets and summer average maximum temperature favoring communities dominated by tarnished plant bugs, and other Hemiptera such as ebony bugs (Figure 4). Grassland in the surrounding area had a positive effect on communities dominated by aphids, and a negative effect on communities dominated by bean leaf beetles, chloropid flies, Japanese beetles, and caterpillars (Figure 4).

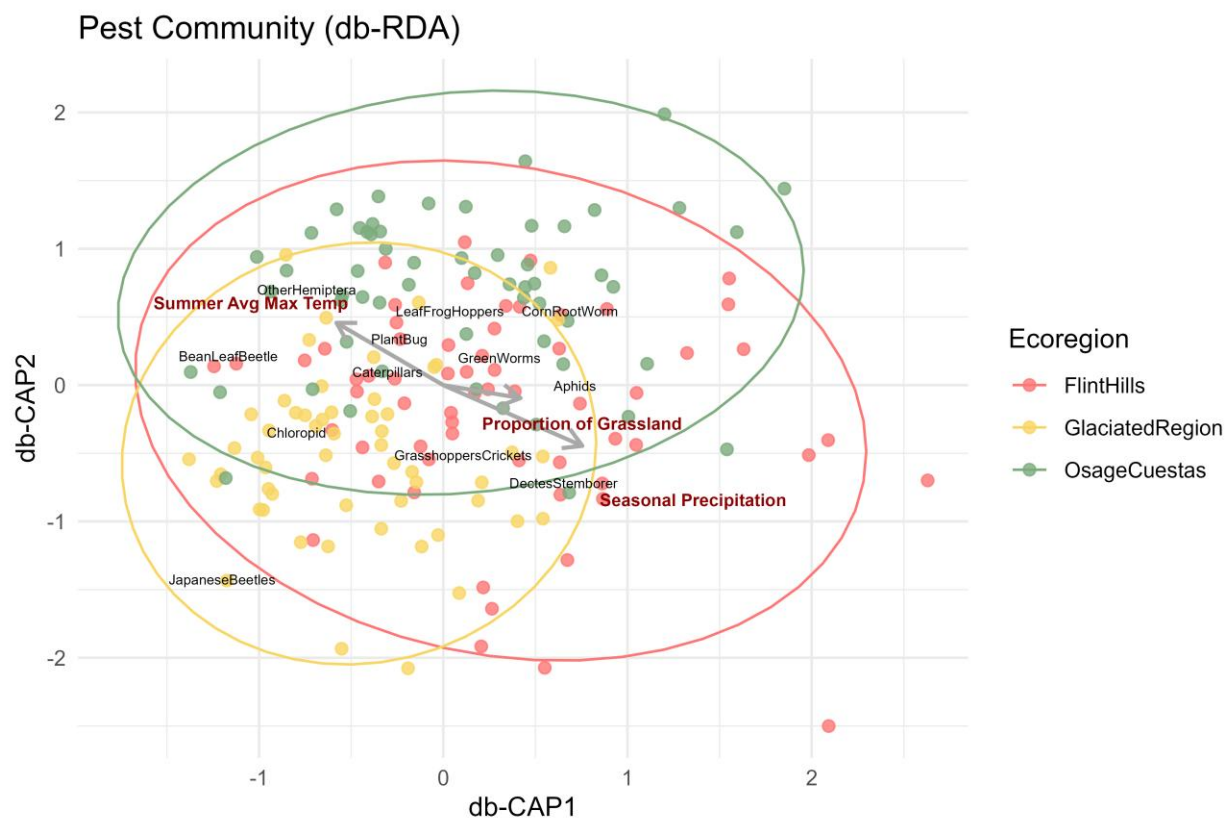


Figure 2-4 Distance-based redundancy analysis (db-RDA) showing the relationship between pest community composition and environmental variables. Environmental vectors represented by gray arrows indicate the direction and relative strength of each variable's effect on community structure. Sites are represented as points, colored by ecoregion, with ellipses which encompass 95% of sites in that grouping. Species/taxa labels are plotted centered on their db-RDA species score.

Landcover and climate effects on predator abundance and community composition

For predators, the percent grass * summer precipitation interaction significantly improved model fit ($\chi^2 = 3.89$, $df = 1$, $p < 0.05$), whereas all other interactions did not ($p \geq 0.142$), supporting an interaction between precipitation and grass cover (candidate model 1). Although ΔAIC for the interaction model fell slightly short of 2 ($\Delta AIC = -1.89$), it had the lowest AIC (ΔAIC range = -0.15 to $+3.74$). We retained the interaction model for inference because our primary goal was hypothesis testing, not prediction, and likelihood ratio test indicated that interaction between precipitation and landcover significantly improved model fit relative to the base additive model providing statistical support for the retention of the interaction term. Predator abundance was negatively affected by the interaction between precipitation and proportion of grassland in the surrounding 1 km landscape (Estimate -0.099 ± 0.049 SE, $p < 0.05$, Table 2). In other words, increasing grass cover had a strong negative impact in areas of high precipitation and a general negative impact with medium precipitation, but this effect was much weaker with low precipitation (Figure 5).

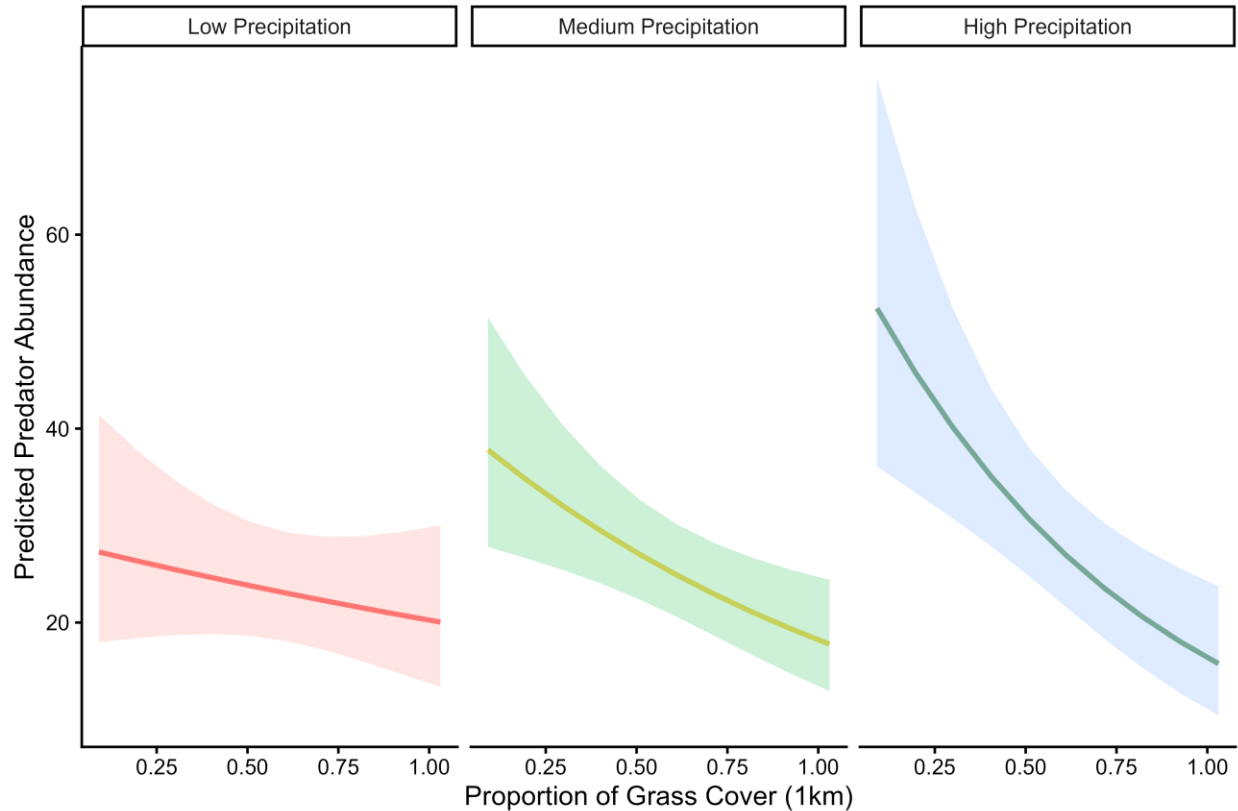


Figure 2-5 Effect of surrounding land cover on pollinators with facet panels showing differing effects at low, medium and high precipitation levels. The solid line represents the model predictions, while the shading indicates 95% confidence intervals. Predictions are presented on the response scale, with all other covariates held at their mean values.

Predator community composition was similarly significantly influenced by landscape and climatic variables, particularly summer precipitation, which explained the greatest proportion of variation ($R^2 = 0.109$, $p = 0.001$), followed by summer maximum temperature ($R^2 = 0.029$, $p = 0.001$) and grassland cover ($R^2 = 0.014$, $p < 0.01$). The db-RDA suggests that environmental variables collectively explained a significant portion of variation in predator community composition ($R^2 = 0.197$, $F_{8,166} = 5.08$, $p = 0.001$), which was spread across two constrained axes (CAP1 and CAP2, $p = 0.001$) and primarily structured by climatic gradients, with precipitation favoring spider- and fly-dominated communities and high summer temperatures favoring ant-

and parasitoid-dominated communities, while landscape position plays a secondary role (Figure 6).

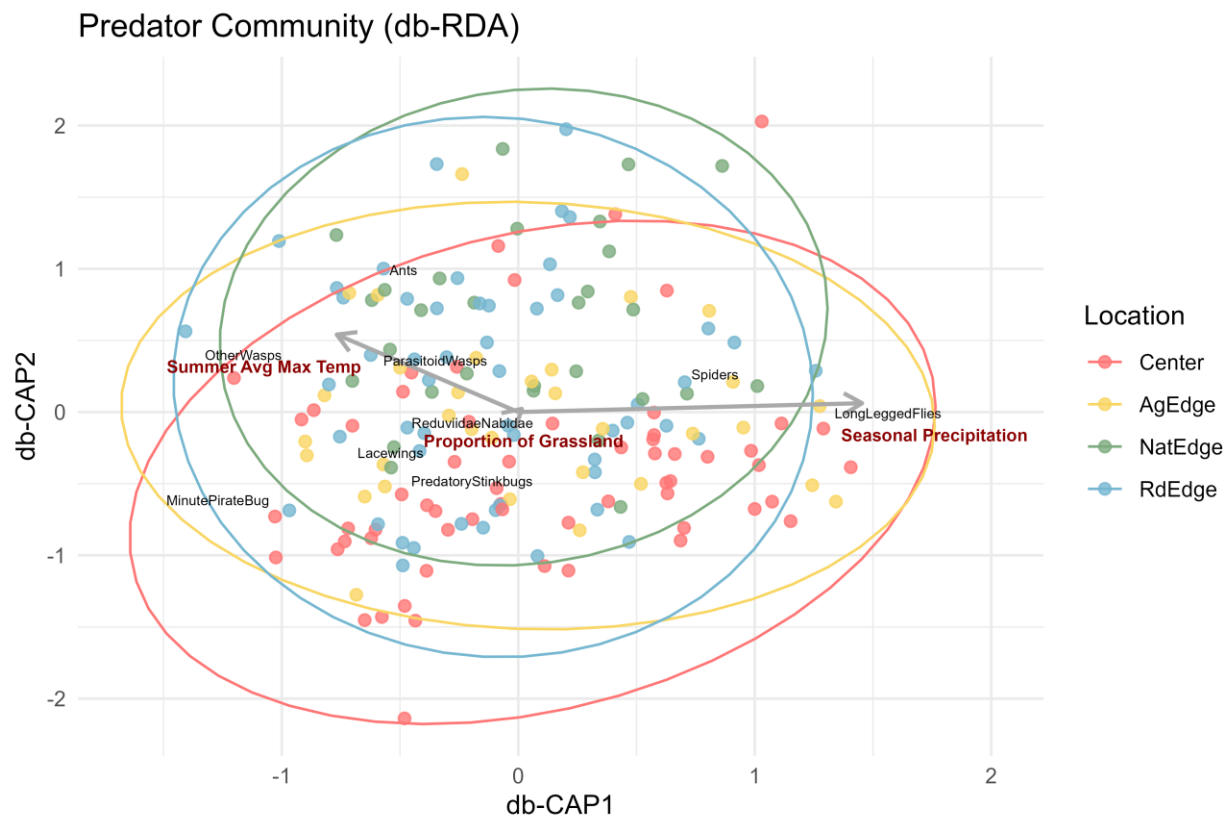


Figure 2-6 Distance-based redundancy analysis (db-RDA) showing the relationship between predator community composition and environmental variables. Environmental vectors represented by gray arrows indicate the direction and relative strength of each variable's effect on community structure. Sites are represented as points, colored by location, with ellipses which encompass 95% of sites in that grouping. Species/taxa labels are plotted centered on their db-RDA species score.

Landcover and climate effects on pollinator abundance and community composition

For pollinators, the percent natural land * summer precipitation interaction model (candidate model 1) significantly improved fit and was the most parsimonious model ($\chi^2 = 4.20$, $df = 1$, $p = 0.040$; $\Delta AIC = -2.20$), while candidate models that included interactions with

location, ecoregion, or temperature showed no significant improvement ($p \geq 0.338$; ΔAIC range = +1.09 to 2.63), indicating a precipitation-dependent effect of grass cover. The interaction between precipitation and proportion of semi-natural land in the surrounding 2 km landscape had a positive effect on pollinators (Estimate 0.196 ± 0.094 SE, $p < 0.05$, Table 2). Specifically, while the effect of semi-natural land was slightly positive with low precipitation, this effect was stronger in areas with medium precipitation and exponential when coupled with high precipitation (Figure 7).

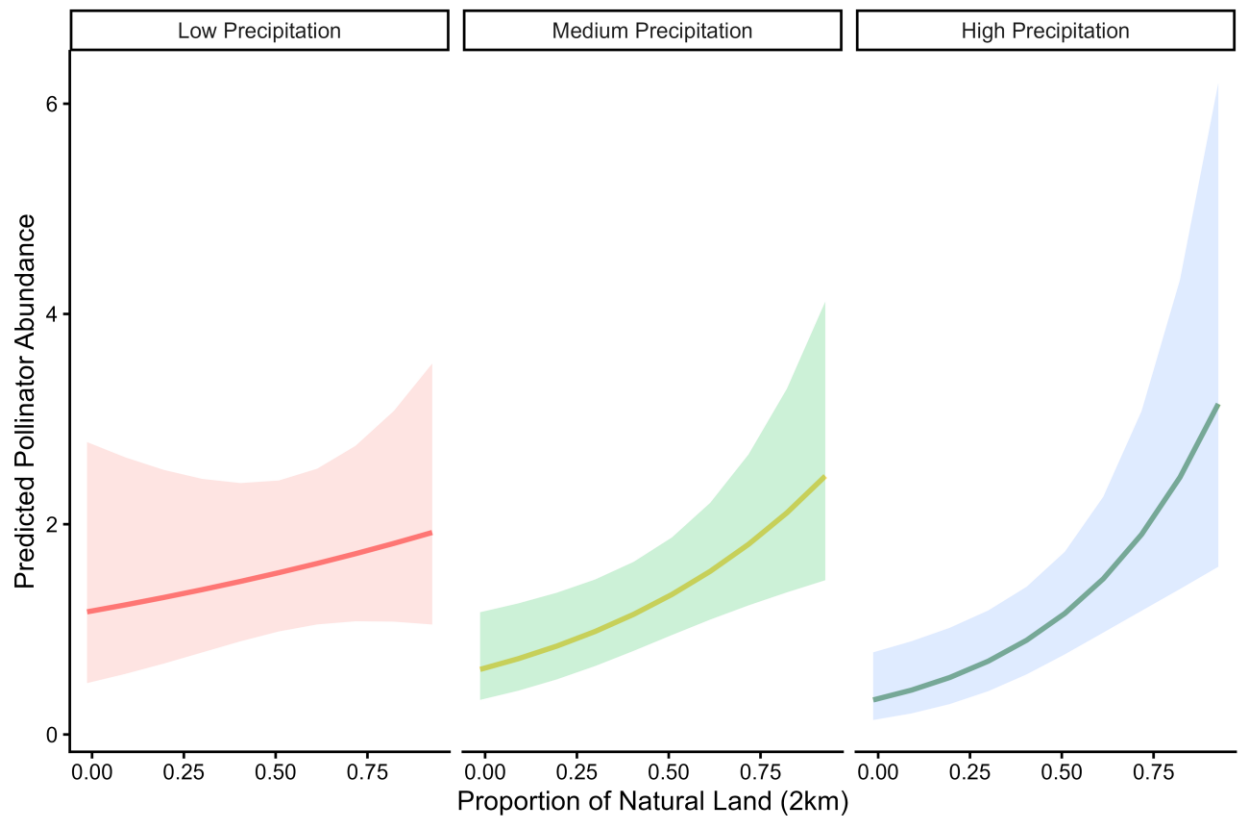


Figure 2-7 Effect of surrounding land cover on pollinators with facet panels showing differing effects at low, medium and high precipitation levels. The solid line represents the model predictions, while the shading indicates 95% confidence intervals. Predictions are presented on the response scale, with all other covariates held at their mean values.

Pollinator community composition was primarily associated with the proportion of semi-natural land cover within 2 km ($R^2 = 0.063$, $p = 0.001$) and summer precipitation ($R^2 = 0.020$, $p < 0.05$), while summer maximum temperature, location, and ecoregion were not significant predictors. The db-RDA suggests that environmental variables collectively explained a significant portion of variation in communities ($R^2 = 0.119$, $F_{8,131} = 2.21$, $p = 0.001$), and the first constrained axis (CAP1) explained a significant portion of variation in pollinator composition ($p < 0.01$), while the second constrained axis (CAP2) was only marginally significant ($p = 0.09$), and further axes were not significant ($p > 0.9$) suggesting that pollinator communities are primarily structured along gradients of semi-natural land cover with marginal effects of precipitation. Proportion of grassland in the surrounding area had a stronger effect on communities dominated by honey bees, and a strong negative effect on hoverflies (Figure 8). Communities dominated by bumble bees were strongly affected by seasonal precipitation, while communities dominated by sweat bees and Megachilidae seem to be negatively affected by seasonal precipitation.

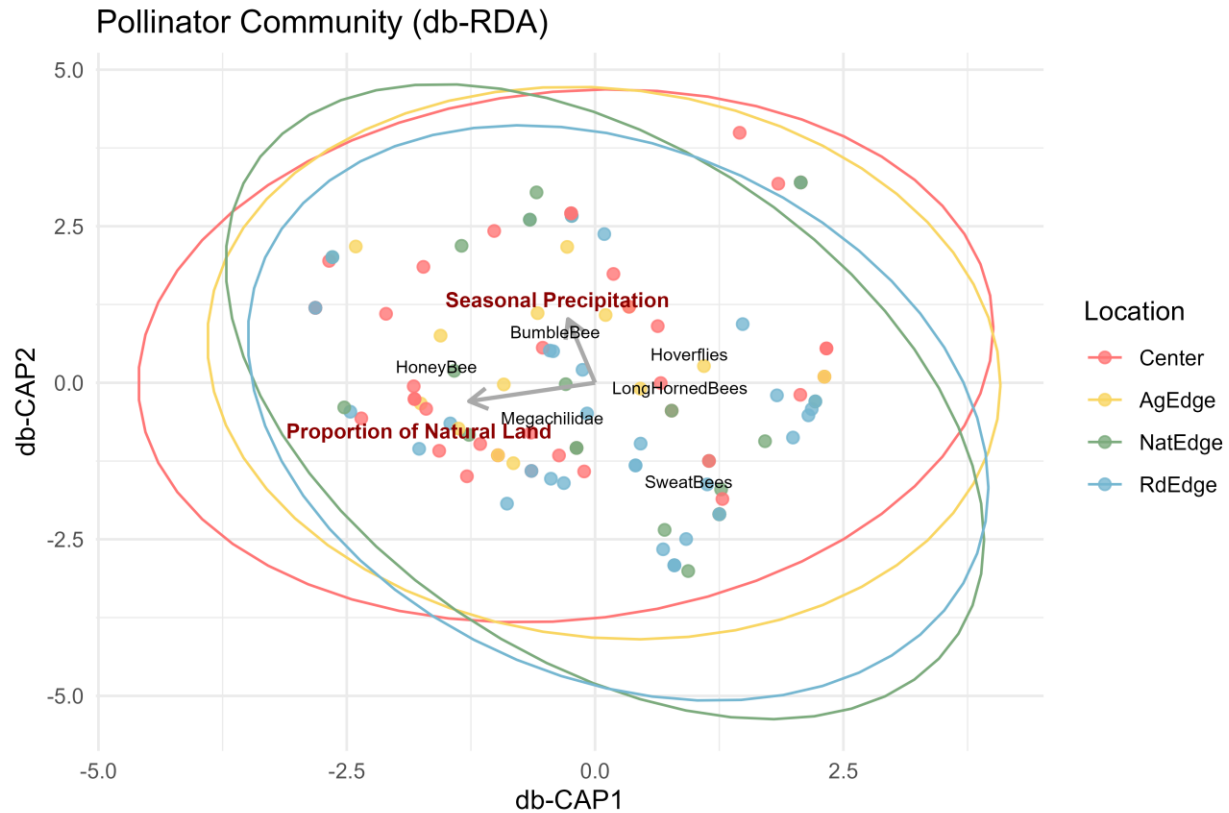


Figure 2-8 Distance-based redundancy analysis (db-RDA) showing the relationship between pollinator community composition and environmental variables. Environmental vectors represented by gray arrows indicate the direction and relative strength of each variable's effect on community structure. Sites are represented as points, colored by location, with ellipses which encompass 95% of sites in that grouping. Species/taxa labels are plotted centered on their db-RDA species score.

Location within field, but not ecoregion, affected insect abundance, while both influenced community composition.

Field location did not interact with land cover variables but had significant main effects on pest, predator, and pollinator abundances. Field centers generally had fewer insects compared to field edges, but the magnitude varied depending on edge type (Table 2, Figure 9). Agricultural edges had significantly more pests (Estimate 0.497 ± 0.110 SE, $p < 0.001$) and predators (Estimate 0.412 ± 0.097 SE, $p < 0.001$) compared to field centers. Road edges and natural edges also had more pests and predators compared to field centers but to a lesser degree than agricultural edges (Pests: road edge estimate 0.324 ± 0.092 SE, $p < 0.001$; semi-natural edge

estimate 0.236 ± 0.119 SE, $p < 0.05$. Predators: road edges estimate = 0.145 ± 0.087 SE, $p < 0.1$, semi-natural edge Estimate 0.285 ± 0.106 SE, $p < 0.01$). In contrast, for pollinators, only their abundance at road edges (Estimate 0.266 ± 0.121 SE, $p < 0.05$) was significantly greater than their abundance the field centers (Table 2, Figure 9).

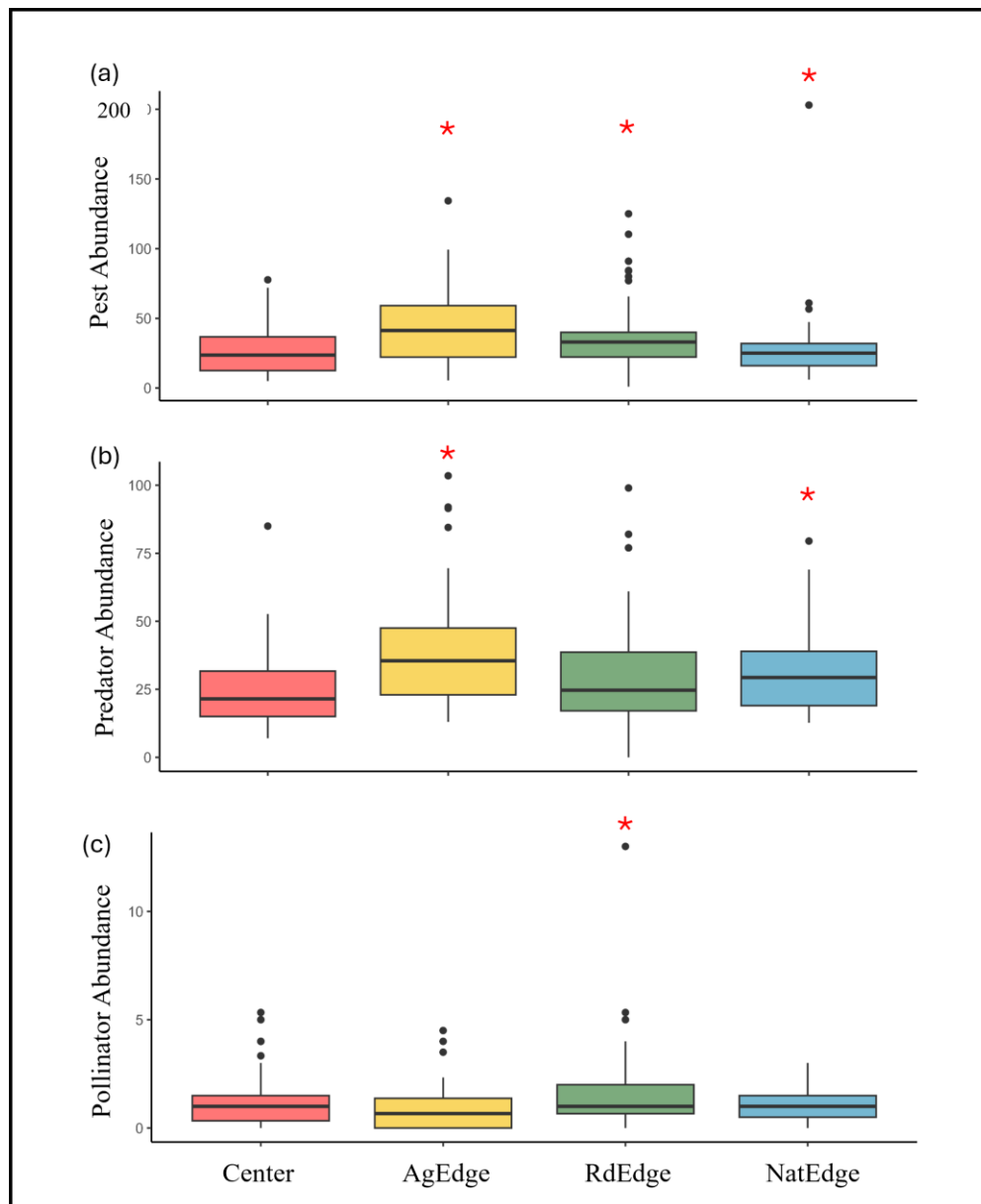


Figure 2-9 Pest (a), predator (b), and pollinator (c) abundance by transect location; center, agricultural edge (AgEdge), road edge (Rd Edge), and natural edge (NatEdge). Boxes show the interquartile range (25th–75th percentiles), with the horizontal line representing the median. Whiskers extend to the most extreme values within 1.5x the interquartile range, and points beyond the whiskers are outliers. Asterisks indicate significant difference from center.

Ecoregion did not significantly explain variation in pest, predator, or pollinator abundance once local landscape composition, weather, and site-level variability were accounted for. Although model coefficients suggested modest differences among ecoregions for pests, these effects were not supported by the overall likelihood ratio test comparing models with and without ecoregion ($\chi^2 = 4.19$, $df = 2$, $p = 0.123$) or by Tukey-adjusted pairwise comparisons among ecoregions (all $p > 0.09$). Predator and pollinator abundance was not influenced by ecoregion, as indicated by a lack of significant effects in the model coefficients and confirmed with a likelihood ratio test (Predators: $\chi^2 = 0.62$, $df = 2$, $p = 0.735$, all pairwise Tukey-adjusted contrasts $p > 0.70$; Pollinators: $\chi^2 = 5.71$, $df = 2$, $p = 0.057$, all pairwise Tukey-adjusted contrasts $p > 0.31$).

Variation in pest and predator community compositions were affected by spatial factors, with both location (pests = $R^2 = 0.038$, $p = 0.001$, predators = $R^2 = 0.044$, $p = 0.001$) and ecoregion (pests = $R^2 = 0.104$, $p = 0.001$, predators = $R^2 = 0.023$, $p < 0.01$) showing strong effects. Community composition of pollinators did not vary with edge type or ecoregion (location: $R^2 = 0.026$, $p = 0.27$; ecoregion: $R^2 = 0.020$, $p = 0.17$).

Discussion

This study was designed to assess the effects of interactions between semi-natural land cover in the surrounding habitat, precipitation, and bordering field edges on insect communities within soybean fields in the Great Plains. Our model results showed that semi-natural land cover in agricultural landscapes reduced pest and predator abundances and increased pollinator abundance. However, this effect was often moderated by seasonal precipitation amounts. Our community composition results indicate that insect community turnover in agroecosystems is

strongly shaped by both climatic and landscape drivers, with differing responses by species and taxa exemplifying varying responses to environmental factors.

Surrounding natural land cover and precipitation

Our study provides evidence that precipitation interacts with the effects of land cover, masking or minimizing the beneficial effects of land cover on insect populations at lower precipitation levels. The amount of grassland cover in the surrounding landscape had a significant negative effect on predators but the magnitude of the effects varied with precipitation where increasing grass cover strongly reduced pest abundance under high precipitation, had a moderate negative effect under medium precipitation, and had a much weaker effect under low precipitation. In contrast, pollinator abundance responded positively to natural land cover across precipitation gradients, with stronger responses in medium and high rainfall areas. For pests, grass cover alone had negative effects on their abundances, irrespective of precipitation amount. Altogether, these results suggest that beneficial insects are more strongly influenced by combined effects of precipitation and land cover and may be more vulnerable than pests during periods of low precipitation.

Our models revealed a significant interaction between precipitation and natural land cover on predator and pollinator abundance. In both cases, low precipitation reduced overall insect abundance as well as the effect of semi-natural land cover. This indicates that when precipitation is low, such as in times of drought or in arid regions, insect populations are reduced to such an extent that it may override any beneficial effects from semi-natural land cover within the landscape. This may be due to a lack of moisture availability, which can affect insects through decreased soil moisture, desiccation, or intermediate effects (Beirne 1970). The benefits

of natural land cover in suppressing pests may be contingent upon adequate precipitation levels. Similar results were found in another study in soybean in Wisconsin where the amount of soybean and habitat diversity affected pest abundances but only in non-drought years (Liere et al. 2015). The interaction with landcover and climate could explain inconsistent effects of natural area on pest suppression across studies that span multiple years or large geographic areas (Liere et al. 2015; Karp et al. 2018).

Pest community composition

The composition of pest communities was most strongly influenced by summer average maximum temperature and seasonal precipitation which affected the abundance and immigration of different insect groups, leading to changing species identity along climate gradients. Fields with high temperatures were dominated by Hemiptera such as plant bugs and ebony bugs. Plant bugs have been shown to respond to higher temperatures with increasing generations within a season, leading to higher abundances of these pests (Altermatt 2009; Ugine 2012). Seasonal precipitation also strongly affected community composition where soybean fields with high precipitation were dominated by *Dectes* stemborers, grasshoppers and crickets. Grasshopper populations have been shown to increase in periods of higher precipitation due to increased available host plant material (Beirne 1970; Whipple et al. 2012; Li et al. 2024). The amount of surrounding grassland also affects pest community composition but to a lesser degree than climate variables. Fields that were surrounded by high amounts of grassland were dominated by aphids which is consistent with previous studies that have found increases in aphid abundance with surrounding seminatural areas in cabbage and sorghum (Martin et al. 2015; Elkins et al. 2022). This could be because neighboring perennial grass can provide alternative host plants and

overwintering grounds for aphids. Contrastingly, in fields surrounded by less grasslands, pest communities were dominated by bean leaf beetles, chloropid flies, Japanese beetles, and caterpillars, perhaps due to lower amounts of host plants for host-specific pests such as bean leaf beetles, and higher predation rates of generalist pests by natural enemies supported by the surrounding grassland, including grassland birds (Tortosa et al. 2023; de Zwaan et al. 2024).

Predator abundance and communities

Contrary to our hypothesis that natural land in the surrounding landscape would increase predator abundances, we found that the amount of grassland in the surrounding landscape had negative effects on predator abundances and the magnitude was stronger with higher precipitation levels. This is unexpected as multiple reviews and meta-analyses have found surrounding non-crop land cover to be beneficial, on average, for natural enemy abundance, diversity and predation activity (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Veres et al. 2013; Rusch et al. 2016). During the time of our study, pest pressure was relatively low, which may be a contributing factor because predator numbers have been shown to respond to pest densities (Haan et al. 2020) and found to disperse when local pest populations are low (Boetzel et al. 2020), therefore our predator numbers could be responding to the available number of pests which is higher in fields with more surrounding agricultural areas and lower in fields with more surrounding grassland. Since many of our predators are generalists, they are likely to be present where there are more prey options, as Liere et al (2015) found with predator abundance in soybean. Furthermore, natural areas may fail to increase predator populations if agricultural practices within the fields themselves counteract the positive effects of natural areas (Tscharncke et al. 2016). Herbicides, commonly used in soybean fields and applied to the fields of this study,

have been found to increase natural enemy mortality as well as decrease their longevity, reproduction, and predation (Zilnik et al. 2023).

It is also possible that the most common predators in our fields (spiders, parasitoid wasps and minute pirate bugs; comprising 81% of the predators) are not as reliant on resources from the surrounding grasslands as other predators such as ants and other wasps, who require alternative food sources from nectar, pollen, or seeds (Patt et al. 1997). However, previous studies have shown that the abundance of spiders, predatory Hemipterans, and parasitoids increase with increasing landscape complexity (Langellotto and Denno 2004). Spider abundance has also been found to significantly increase with surrounding semi-natural areas, although the effect on parasitoid and predatory beetle abundances was inconclusive (Shackelford et al. 2013). Therefore, it is possible that different natural enemy taxa are responding differently to changes in land cover and surrounding semi-natural areas.

Predator community composition in our study was more strongly associated with climatic variables than with landscape structure, indicating that interannual variation in precipitation and temperature plays a key role in shaping predator assemblages. Climatic conditions can directly influence predator phenology, survival, and activity (Durant et al. 2007), as well as indirectly affect communities through changes in prey availability (Zhu et al. 2015). Therefore, biodiversity and niche redundancy may be especially important for maintaining predator community resilience, because simplified predator assemblages are likely to be more vulnerable to climate-driven population declines, reducing their ability to provide consistent pest suppression (Yachi and Loreau 1999; Cardinale et al. 2012). Landscape heterogeneity and habitat complexity can partially buffer these climatic effects by supporting higher biodiversity within predator communities (Landis et al. 2000; Tscharntke et al. 2012; Rusch et al. 2016).

Pollinator abundance and communities

Pollinator abundances were affected by the interaction between natural land cover and precipitation. Specifically, as the amount of natural land cover surrounding a soybean field increased, the abundance of pollinators increased as well. However, the magnitude of the effects increased with precipitation. Precipitation could be especially important for pollinators, magnifying the effects of natural land through positive effects on floral resources on which pollinators rely. Many pollinators also rely on surrounding natural land for nesting habitat and other resources, such as water.

Pollinator community composition was affected by natural land cover and precipitation independently (i.e., no significant interaction). Pollinator communities in areas with lower amounts of surrounding natural areas were dominated by hoverflies, while areas with high surrounding natural areas were dominated by honeybees. A similar response was reported by Jauker et al. (2009), who found that bee abundance declined in response to a reduction of natural grassland in the area surrounding agricultural fields, hoverfly abundance increased. Honeybees, with a confined foraging range, respond positively to alternative foraging resources near fields that can provide nectar when soybean is not flowering. Hoverflies forage across larger distances than bees, are not limited to a specific home range since they require pollen for adult nutrition rather than for provisioning their offspring (Rader et al. 2016), and many hoverfly larvae consume aphids which are commonly found in agricultural fields (Jauker et al. 2009).

There is hope that hoverfly populations may be more resilient to current trends in land use change, providing pollination for crops in areas with lower amounts of surrounding natural areas, but many species require specific microhabitats for larval development which rely on

supplementary resources (Jauker et al. 2009) and hedgerows are suggested as a management tactic to encourage pollination by hoverflies (Doyle et al. 2020). Still, this shift in pollinator communities along a natural land gradient may have implications for pollination and fruit set in dense agricultural areas, as hoverflies do not pollinate as effectively as bees, requiring higher visitation rates (Rader et al. 2016).

Precipitation also affected bee community composition where sites with greater seasonal precipitation supported more bumble bees and less sweat bees. Previous studies have shown that bumble bees have a strong response to precipitation, possibly moderated by reductions in floral resources and subpar nesting conditions with nest density declines in drought years likely due to reduced floral resources and lack of suitable nesting conditions (Thuma et al. 2025). Decreases in floral display size and nectar rewards under drought conditions have been linked to reduced bumble bee visitation (Kuppler et al. 2021). Additionally, comparative physiological studies have shown that larger bees such as bumble bees are more prone to desiccation than smaller sweat bees (Burdine and McCluney 2019).

Field edges

In addition to landscape composition, previous work has shown that the structure of field edges strongly influences insect communities in agricultural landscapes (Kross et al. 2020; Rischen et al. 2023). Complex semi-natural borders often support higher abundance and diversity of pollinators and predators than simplified or agricultural borders (J. Holland and Fahrig 2000; Meek et al. 2002; Campbell et al. 2017). Conversely, pest abundance often increases along agricultural boundaries that facilitate colonization from neighboring fields (Haan et al. 2020; Kennedy and Huseeth 2022). Our results mostly align with these patterns: pest abundance was

highest at field edges, particularly those adjacent to other agricultural fields, with predators tracking pest abundances at those edges, and pollinator abundance significantly increased along road margins which were typically grassy and often contained wildflowers.

Effects of local edges can sometimes be mediated by an interaction with surrounding landscape context (Akter et al. 2023). For example, Boetzel et al. (2020) found that adjacent natural land enhanced activity by predatory arthropods at field borders, and that distance functions for parasitoids and pests were influenced by the surrounding semi-natural land. Evans et al. (2016) reported that landscape complexity increased invertebrate diversity primarily at field edges and concluded that field edges should be considered alongside landscape mosaic for biodiversity enhancement. In our study, although we found significant edge effects, we did not find any significant interaction effect between field edge types and the proportion of natural area in the surrounding landscape, suggesting that land cover effects influence insects similarly across the soybean fields.

Conclusion

Our results have implications for agriculture in that surrounding seminatural land cover is beneficial through a reduction in pest numbers and an increase in pollinator numbers, but the effects may be lost under low precipitation, for example, in years of drought or areas of low precipitation. Therefore, the lack of consistent results in previous studies, especially when comparing studies across a global scale, could be due to interannual changes in precipitation across years, spatial differences in precipitation across locations, or a combination of both. Changes in precipitation, both spatially and temporally, can affect the ecosystem services provided by natural areas, which will be able to provide more pollination services and lower pest

pressure under moderate and higher precipitation conditions. In our study, predators seem to be more susceptible to precipitation changes than pests, which could lead to an inability to suppress pest populations during low precipitation, perhaps even if larger amounts of surrounding natural areas are present.

From a management perspective, these findings add to the body of work supporting the recommendation of maintaining seminatural land cover and landscape heterogeneity to bolster natural enemy and pollinator populations, while recognizing that climatic conditions may amplify or suppress pest-predator interactions, underscoring the need for context specific, adaptive strategies to sustain natural biological control. As climate changes, many areas are predicted to experience increased drought, which seems to disproportionately affect beneficial insects, and the benefits of natural areas on pest suppression might be reduced. Therefore, employing additional local management tactics to support natural predators will be important.

Because pests are more abundant on edges, particularly at agricultural edges, after sufficient monitoring, it could be sufficient to target pest management at specific edges rather than the entire field. This would allow growers to substantially reduce chemical input while still addressing insect pest concerns. Additionally, establishing semi-natural field borders such as hedgerows or grass strips may reduce pest pressure compared to agricultural borders (Akter et al. 2023). Overall, our findings support the view that agricultural insect communities are strongly influenced by the surrounding landscape mosaic and that strategically managing edge vegetation and semi-natural land cover in concert can strengthen pollination and pest-regulation services while reducing pest spillover in soybean systems.

The effect of the interaction between landscape and climate could be masking significant landscape effects on insect abundance and community composition in other studies where it is not considered, and possibly hindering us from developing effective, ecologically sound strategies for integrating natural land cover areas into agroecosystems. These results highlight the importance of incorporating seasonal precipitation and its interaction with landscape composition into future ecological models to accurately assess relationships between landscape composition and insect abundance and community composition to promote effective management strategies.

References

- Akter, Salma, Syed Z. M. Rizvi, Ahsanul Haque, et al. 2023. "Continent-wide Evidence That Landscape Context Can Mediate the Effects of Local Habitats on In-field Abundance of Pests and Natural Enemies." *Ecology and Evolution* 13 (1): e9737. <https://doi.org/10.1002/ece3.9737>.
- Altermatt, Florian. 2009. "Climatic Warming Increases Voltinism in European Butterflies and Moths." *Proceedings of the Royal Society B: Biological Sciences* 277 (1685): 1281–87. <https://doi.org/10.1098/rspb.2009.1910>.
- Balfour, Nicholas J., and Francis L. W. Ratnieks. 2025. "Wind Alters Plant-Pollinator Community Structure, Bee Foraging Rate & Movements Between Plants." *Behavioral Ecology*, June 15, araf067. <https://doi.org/10.1093/beheco/araf067>.
- Bannwart, Paul, Antoine Gardarin, and Sandrine Petit. 2025. "Do Semi-Natural Habitats Enhance Overwintering of Generalist Predators in Arable Cropping Systems? A Meta-Analysis." *Biological Control* 201 (February): 105700. <https://doi.org/10.1016/j.biocontrol.2025.105700>.
- Beirne, Bryan P. 1970. "EFFECTS OF PRECIPITATION ON CROP INSECTS." *The Canadian Entomologist* 102 (11): 1360–73. <https://doi.org/10.4039/Ent1021360-11>.
- Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. "Sustainable Pest Regulation in Agricultural Landscapes: A Review on Landscape Composition, Biodiversity and Natural Pest Control." *Proceedings. Biological Sciences* 273 (1595): 1715–27. <https://doi.org/10.1098/rspb.2006.3530>.
- Biegerl, Carolin, Andrea Holzschuh, Benjamin Tanner, et al. 2025. "Landscape Management Can Foster Pollinator Richness in Fragmented High-Value Habitats." *Proceedings of the Royal Society B: Biological Sciences* 292 (2040): 20242686. <https://doi.org/10.1098/rspb.2024.2686>.
- Boetzel, Fabian A., Maren Schuele, Jochen Krauss, and Ingolf Steffan-Dewenter. 2020. "Pest Control Potential of Adjacent Agri-Environment Schemes Varies with Crop Type and Is Shaped by Landscape Context and within-Field Position." *Journal of Applied Ecology* 57 (8): 1482–93. <https://doi.org/10.1111/1365-2664.13653>.
- Boetzel, Fabian A., Douglas Sponsler, Matthias Albrecht, et al. 2024. "Distance Functions of Carabids in Crop Fields Depend on Functional Traits, Crop Type and Adjacent Habitat: A Synthesis." *Proceedings. Biological Sciences* 291 (2014): 20232383. <https://doi.org/10.1098/rspb.2023.2383>.
- Bolker, Benjamin M., Mollie E. Brooks, Connie J. Clark, et al. 2009. "Generalized Linear Mixed Models: A Practical Guide for Ecology and Evolution." *Trends in Ecology & Evolution* 24 (3): 127–35. <https://doi.org/10.1016/j.tree.2008.10.008>.

Bosem Baillod, Aliette, Teja Tscharntke, Yann Clough, and Péter Batáry. 2017. “Landscape-Scale Interactions of Spatial and Temporal Cropland Heterogeneity Drive Biological Control of Cereal Aphids.” *Journal of Applied Ecology* 54 (6): 1804–13. <https://doi.org/10.1111/1365-2664.12910>.

Brittain, Claire, Claire Kremen, and Alexandra-Maria Klein. 2013. “Biodiversity Buffers Pollination from Changes in Environmental Conditions.” *Global Change Biology* 19 (2): 540–47. <https://doi.org/10.1111/gcb.12043>.

Brooks, Mollie E., Kasper Kristensen, Koen J. van Benthem, et al. 2017. “glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling.” *The R Journal* 9 (2): 378–400. <https://doi.org/10.32614/RJ-2017-066>.

Burdine, Justin D., and Kevin E. McCluney. 2019. “Differential Sensitivity of Bees to Urbanization-Driven Changes in Body Temperature and Water Content.” *Scientific Reports* 9 (1): 1643. <https://doi.org/10.1038/s41598-018-38338-0>.

Burnham, Kenneth P., and David R. Anderson, eds. 2004. *Model Selection and Multimodel Inference*. Springer. <https://doi.org/10.1007/b97636>.

Campbell, Alistair, Andrew Wilby, Peter Sutton, and Felix Wäckers. 2017. “Do Sown Flower Strips Boost Wild Pollinator Abundance and Pollination Services in a Spring-Flowering Crop? A Case Study from UK Cider Apple Orchards.” *Agriculture, Ecosystems & Environment* 239 (February): 20–29. <https://doi.org/10.1016/j.agee.2017.01.005>.

Cardinale, Bradley J., J. Emmett Duffy, Andrew Gonzalez, et al. 2012. “Biodiversity Loss and Its Impact on Humanity.” *Nature* 486 (7401): 59–67. <https://doi.org/10.1038/nature11148>.

Carrié, Romain, Johan Ekroos, and Henrik G. Smith. 2018. “Organic Farming Supports Spatiotemporal Stability in Species Richness of Bumblebees and Butterflies.” *Biological Conservation* 227 (November): 48–55. <https://doi.org/10.1016/j.biocon.2018.08.022>.

Chaplin-Kramer, Rebecca, Megan E. O’Rourke, Eleanor J. Blitzer, and Claire Kremen. 2011. “A Meta-Analysis of Crop Pest and Natural Enemy Response to Landscape Complexity.” *Ecology Letters* 14 (9): 922–32. <https://doi.org/10.1111/j.1461-0248.2011.01642.x>.

Checkoff. 2023. “New Study Finds U.S. Soybean Industry Has \$124 Billion Impact on the United States Economy.” United Soybean Board, August 29. <https://unitedsoybean.org/hopper/new-study-finds-u-s-soybean-industry-has-124-billion-impact-on-the-united-states-economy/>.

Chen, Bowen. 2020. “CropScapeR: Access Cropland Data Layer Data via the ‘CropScape’ Web Service.” June 29. <https://doi.org/10.32614/CRAN.package.CropScapeR>.

Clem, C. Scott, and Alexandra N. Harmon-Threatt. 2021. “Field Borders Provide Winter Refuge for Beneficial Predators and Parasitoids: A Case Study on Organic Farms.” *Journal of Insect Science* 21 (3): 2. <https://doi.org/10.1093/jisesa/ieab027>.

Cohen, Abigail, James Devries, and Paul Galpern. 2023. “Wetland Cover in Agricultural Landscapes Is Positively Associated with Bumblebee Abundance.” *Insect Conservation and Diversity* 17 (November). <https://doi.org/10.1111/icad.12701>.

Courson, Emeric, Sandrine Petit, Sylvain Poggi, and Benoit Ricci. 2022. “Weather and Landscape Drivers of the Regional Level of Pest Occurrence in Arable Agriculture: A Multi-Pest Analysis at the French National Scale.” *Agriculture, Ecosystems & Environment* 338 (October): 108105. <https://doi.org/10.1016/j.agee.2022.108105>.

Daniel, Folashade, Hong Ooi, Rich Calaway, Microsoft, and Steve Weston. 2022. *Foreach: Provides Foreach Looping Construct*. V. 1.5.2. Released February 2. <https://cran.r-project.org/web/packages/foreach/index.html>.

Deutsch, Curtis A., Joshua J. Tewksbury, Michelle Tigchelaar, et al. 2018. “Increase in Crop Losses to Insect Pests in a Warming Climate.” *Science* 361 (6405): 916–19. <https://doi.org/10.1126/science.aat3466>.

Doyle, Toby, Will L. S. Hawkes, Richard Massy, Gary D. Powney, Myles H. M. Menz, and Karl R. Wotton. 2020. “Pollination by Hoverflies in the Anthropocene.” *Proceedings of the Royal Society B: Biological Sciences* 287 (1927): 20200508. <https://doi.org/10.1098/rspb.2020.0508>.

Durant, Joel, Geir Ottersen, and Nils Chr Stenseth. 2007. “Climate and the Match or Mismatch between Predator Requirements and Resource Availability.” *Climate Research* 33 (April): 271–83. <https://doi.org/10.3354/cr033271>.

Ekroos, Johan, Maj Rundlöf, and Henrik G. Smith. 2013. “Trait-Dependent Responses of Flower-Visiting Insects to Distance to Semi-Natural Grasslands and Landscape Heterogeneity.” *Landscape Ecology* 28 (7): 1283–92. <https://doi.org/10.1007/s10980-013-9864-2>.

Elkins, Blake H., Micky D. Eubanks, Ashleigh M. Faris, Hsiao-Hsuan Wang, and Michael J. Brewer. 2022. “Landscape Complexity Has Mixed Effects on an Invasive Aphid and Its Natural Enemies in Sorghum Agroecosystems.” *Environmental Entomology* 51 (4): 660–69. <https://doi.org/10.1093/ee/nvac036>.

Evans, Tracy R., Meredith J. Mahoney, Everett D. Cashatt, Jinze Noordijk, Geert De Snoo, and C. J. M. Musters. 2016. “The Impact of Landscape Complexity on Invertebrate Diversity in Edges and Fields in an Agricultural Area.” *Insects* 7 (1): 7. <https://doi.org/10.3390/insects7010007>.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. Third edition. Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

Fox, John. 2015. *Applied Regression Analysis and Generalized Linear Models*. SAGE Publications.

Fox, John, and Georges Monette. 1992. “Generalized Collinearity Diagnostics.” *Journal of the American Statistical Association* 87 (417): 178–83. <https://doi.org/10.1080/01621459.1992.10475190>.

Fricke, Ute, Ingolf Steffan-Dewenter, Jie Zhang, et al. 2022. “Landscape Diversity and Local Temperature, but Not Climate, Affect Arthropod Predation among Habitat Types.” *PloS One* 17 (4): e0264881. <https://doi.org/10.1371/journal.pone.0264881>.

Gomez Villegas, Araceli, Hannah E. Stowe, Abigail Lyons, Rachele Dailey, Julie A. Peterson, and Autumn Smart. 2025. “Community Composition and Abundance of Wild Bees at Row Crop-Grassland Interfaces in West Central Nebraska.” *Environmental Entomology* 54 (3): 632–43. <https://doi.org/10.1093/ee/nvaf040>.

González, Ezequiel, Adriana Salvo, María Teresa Defagó, and Graciela Valladares. 2016. “A Moveable Feast: Insects Moving at the Forest-Crop Interface Are Affected by Crop Phenology and the Amount of Forest in the Landscape.” *PloS One* 11 (7): e0158836. <https://doi.org/10.1371/journal.pone.0158836>.

González-Tokman, Daniel, Alex Córdoba-Aguilar, Wesley Dáttilo, Andrés Lira-Noriega, Rosa A. Sánchez-Guillén, and Fabricio Villalobos. 2020. “Insect Responses to Heat: Physiological Mechanisms, Evolution and Ecological Implications in a Warming World.” *Biological Reviews of the Cambridge Philosophical Society* 95 (3): 802–21. <https://doi.org/10.1111/brv.12588>.

Guo, Fengyi, Jonathan Lenoir, and Timothy C. Bonebrake. 2018. “Land-Use Change Interacts with Climate to Determine Elevational Species Redistribution.” *Nature Communications* 9 (1): 1315. <https://doi.org/10.1038/s41467-018-03786-9>.

Gurr, Geoff M., Steve D. Wratten, Douglas A. Landis, and Minsheng You. 2017. “Habitat Management to Suppress Pest Populations: Progress and Prospects.” *Annual Review of Entomology* 62 (January): 91–109. <https://doi.org/10.1146/annurev-ento-031616-035050>.

Haan, Nathan L., Yajun Zhang, and Douglas A. Landis. 2020. “Predicting Landscape Configuration Effects on Agricultural Pest Suppression.” *Trends in Ecology & Evolution* 35 (2): 175–86. <https://doi.org/10.1016/j.tree.2019.10.003>.

Harman, Rachel R., and Tania N. Kim. 2024. “Differentiating Spillover: An Examination of Cross-Habitat Movement in Ecology.” *Proceedings of the Royal Society B: Biological Sciences* 291 (2016): 20232707. <https://doi.org/10.1098/rspb.2023.2707>.

Hart, Edmund, and Kendon Bell. 2015. Prism: Access Data from the Oregon State Prism Climate Project. Zenodo, released November 12. <https://doi.org/10.5281/ZENODO.33663>.

Hartig, F. 2025. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. Released. R package version 0.4.7. <<http://florianhartig.github.io/DHARMA/>>.

Harvey, Jeffrey A., Robin Heinen, Rieta Gols, and Madhav P. Thakur. 2020. “Climate Change-mediated Temperature Extremes and Insects: From Outbreaks to Breakdowns.” *Global Change Biology* 26 (12): 6685–701. <https://doi.org/10.1111/gcb.15377>.

Hijmans, Robert J., Márcia Barbosa, Roger Bivand, et al. 2025. Terra: Spatial Data Analysis. V. 1.8-54. Released June 1. <https://cran.r-project.org/web/packages/terra/index.html>.

Hijmans, Robert J., Jacob van Etten, Michael Sumner, et al. 2025. Raster: Geographic Data Analysis and Modeling. V. 3.6-32. Released March 28. <https://cran.r-project.org/web/packages/raster/index.html>.

Holland, J. M., H. Oaten, S. Moreby, et al. 2012. “Agri-Environment Scheme Enhancing Ecosystem Services: A Demonstration of Improved Biological Control in Cereal Crops.” *Agriculture, Ecosystems & Environment* 155 (July): 147–52. <https://doi.org/10.1016/j.agee.2012.04.014>.

Holland, Jeffrey, and Lenore Fahrig. 2000. “Effect of Woody Borders on Insect Density and Diversity in Crop Fields: A Landscape-Scale Analysis.” *Agriculture, Ecosystems & Environment* 78 (April): 115–22. [https://doi.org/10.1016/S0167-8809\(99\)00123-1](https://doi.org/10.1016/S0167-8809(99)00123-1).

Holland, John M, Felix JJA Bianchi, Martin H. Entling, Anna-Camilla Moonen, Barbara M. Smith, and Philippe Jeanneret. 2016. “Structure, Function and Management of Semi-Natural Habitats for Conservation Biological Control: A Review of European Studies.” *Pest Management Science* 72 (9): 1638–51. <https://doi.org/10.1002/ps.4318>.

Holzschuh, Andrea, Carsten F. Dormann, Teja Tscharncke, and Ingolf Steffan-Dewenter. 2013. “Mass-Flowering Crops Enhance Wild Bee Abundance.” *Oecologia* 172 (2): 477–84. <https://doi.org/10.1007/s00442-012-2515-5>.

Iuliano, Benjamin, and Claudio Gratton. 2020. “Temporal Resource (Dis)Continuity for Conservation Biological Control: From Field to Landscape Scales.” *Frontiers in Sustainable Food Systems* 4 (September). <https://doi.org/10.3389/fsufs.2020.00127>.

Jauker, Frank, Tim Diekötter, Franziska Schwarzbach, and Volkmar Wolters. 2009. “Pollinator Dispersal in an Agricultural Matrix: Opposing Responses of Wild Bees and Hoverflies to Landscape Structure and Distance from Main Habitat.” *Landscape Ecology* 24 (4): 547–55. <https://doi.org/10.1007/s10980-009-9331-2>.

Kansas Geological Survey. 2025. “Physiographic Regions.” GeoKansas. <https://geokansas.ku.edu/physiographic-regions>.

Kansas Native Plant Society. 2021. “Ecoregions.” Kansas Native Plant Society.
<https://www.kansasnativeplantsociety.org/ecoregions/>.

Karp, Daniel S., Rebecca Chaplin-Kramer, Timothy D. Meehan, et al. 2018. “Crop Pests and Predators Exhibit Inconsistent Responses to Surrounding Landscape Composition.” *Proceedings of the National Academy of Sciences* 115 (33): E7863–70.
<https://doi.org/10.1073/pnas.1800042115>.

Kennedy, George G., and Anders S. Huseeth. 2022. “Pest Species Respond Differently to Farm Field Size.” *Proceedings of the National Academy of Sciences of the United States of America* 119 (39): e2214082119. <https://doi.org/10.1073/pnas.2214082119>.

Klaus, Felix, Teja Tschardt, Johannes Uhler, and Ingo Grass. 2021. “Calcareous Grassland Fragments as Sources of Bee Pollinators for the Surrounding Agricultural Landscape.” *Global Ecology and Conservation* 26 (January): e01474.
<https://doi.org/10.1016/j.gecco.2021.e01474>.

Knapp, Michal, and Milan Řezáč. 2015. “Even the Smallest Non-Crop Habitat Islands Could Be Beneficial: Distribution of Carabid Beetles and Spiders in Agricultural Landscape.” *PloS One* 10 (4): e0123052. <https://doi.org/10.1371/journal.pone.0123052>.

Kremen, Claire, Neal Williams, Robert Bugg, John Fay, and Robin Thorp. 2004. “The Area Requirements of an Ecosystem Service: Crop Pollination by Native Bee Communities in California.” *Ecology Letters* 7 (November): 1109–19. <https://doi.org/10.1111/j.1461-0248.2004.00662.x>.

Kross, Sara M., Breanna L. Martinico, Ryan P. Bourbour, Jason M. Townsend, Chris McColl, and T. Rodd Kelsey. 2020. “Effects of Field and Landscape Scale Habitat on Insect and Bird Damage to Sunflowers.” *Frontiers in Sustainable Food Systems* 4 (April).
<https://doi.org/10.3389/fsufs.2020.00040>.

Kuppler, J., J. Wieland, R. R. Junker, and M. Ayasse. 2021. “Drought-Induced Reduction in Flower Size and Abundance Correlates with Reduced Flower Visits by Bumble Bees.” *AoB PLANTS* 13 (1). <https://doi.org/10.1093/aobpla/plab001>.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. “Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture.” *Annual Review of Entomology* 45: 175–201. <https://doi.org/10.1146/annurev.ento.45.1.175>.

Langellotto, Gail A., and Robert F. Denno. 2004. “Responses of Invertebrate Natural Enemies to Complex-Structured Habitats: A Meta-Analytical Synthesis.” *Oecologia* 139 (1): 1–10. <https://doi.org/10.1007/s00442-004-1497-3>.

Lavandero, Blas, Enrique Maldonado-Santos, Estefania Muñoz-Quilodran, et al. 2025. “Interaction Effects of Farm-Scale Management of Natural Enemy Resources and the

Surrounding Seminatural Habitat on Insect Biological Control.” *Insects* 16 (3): 3.
<https://doi.org/10.3390/insects16030286>.

Legendre, Pierre, and Eugene D. Gallagher. 2001. “Ecologically Meaningful Transformations for Ordination of Species Data.” *Oecologia* 129 (2): 271–80.
<https://doi.org/10.1007/s004420100716>.

Leibold, Mathew, Marcel Holyoak, Nicolas Mouquet, et al. 2004. “The Metacommunity Concept: A Framework for Multi-Scale Community Ecology.” *Ecology Letters* 7 (July): 601–13.
<https://doi.org/10.1111/j.1461-0248.2004.00608.x>.

Li, Yonghui, Qing Liu, Xiaoming Zhang, et al. 2024. “Effects of Environmental Factors on the Diversity of Grasshopper Communities along Altitude Gradients in Xizang, China.” *Insects* 15 (9): 671. <https://doi.org/10.3390/insects15090671>.

Liere, Heidi, Tania N. Kim, Benjamin P. Werling, Timothy D. Meehan, Douglas A. Landis, and Claudio Gratton. 2015. “Trophic Cascades in Agricultural Landscapes: Indirect Effects of Landscape Composition on Crop Yield.” *Ecological Applications* 25 (3): 652–61.
<https://doi.org/10.1890/14-0570.1>.

Lisic, Jonathan, Lu Chen, and Jemma Stachelek. 2024. *cdlTools: Tools to Download and Work with USDA Cropscape Data*. V. 1.13. Released March 23. <https://cran.r-project.org/web/packages/cdlTools/index.html>.

Lüdecke, Daniel. 2018. “Ggeffects: Tidy Data Frames of Marginal Effects from Regression Models.” *Journal of Open Source Software* 3 (26): 772.
<https://doi.org/10.21105/joss.00772>.

Ma, Chun-Sen, Bing-Xin Wang, Xue-Jing Wang, et al. 2025. “Crop Pest Responses to Global Changes in Climate and Land Management.” *Nature Reviews Earth & Environment* 6 (4): 264–83. <https://doi.org/10.1038/s43017-025-00652-3>.

Magagnoli, Serena, Sara Bosi, Lorenzo Negri, Giovanni Dinelli, Giovanni Burgio, and Antonio Masetti. 2024. “Flowering Areas Enhance Insect Pollinators and Biological Control Agents in Wheat Intensive Agro-ecosystems.” *Insect Conservation and Diversity* 17 (June).
<https://doi.org/10.1111/icad.12757>.

Martin, Emily A., Björn Reineking, Bumsuk Seo, and Ingolf Steffan-Dewenter. 2013. “Natural Enemy Interactions Constrain Pest Control in Complex Agricultural Landscapes.” *Proceedings of the National Academy of Sciences of the United States of America* 110 (14): 5534–39. <https://doi.org/10.1073/pnas.1215725110>.

Martin, Emily A., Björn Reineking, Bumsuk Seo, and Ingolf Steffan-Dewenter. 2015. “Pest Control of Aphids Depends on Landscape Complexity and Natural Enemy Interactions.” *PeerJ* 3 (July): e1095. <https://doi.org/10.7717/peerj.1095>.

- Meek, Bill, Dick Loxton, Tim Sparks, Richard Pywell, Heather Pickett, and Marek Nowakowski. 2002. "The Effect of Arable Field Margin Composition on Invertebrate Biodiversity." *Biological Conservation* 106 (2): 259–71. [https://doi.org/10.1016/S0006-3207\(01\)00252-X](https://doi.org/10.1016/S0006-3207(01)00252-X).
- Monnett, Evan, and Christina Stone. 2025. "The Heart of the American Heartlands." U.S. Fish & Wildlife Service, April 4. <https://www.fws.gov/story/2025-04/heart-american-heartlands>.
- National Agricultural Statistics Service. 2025. Acreage Report - June 30 2025. Acreage Report Nos. 1949–1522. United States Department of Agriculture. <https://www.nass.usda.gov/Newsroom/2025/06-30-2025.php>.
- Nunez, Sarahi, and Rob Alkemade. 2021. "Exploring Interaction Effects from Mechanisms between Climate and Land-Use Changes and the Projected Consequences on Biodiversity." *Biodiversity and Conservation* 30 (12): 3685–96. <https://doi.org/10.1007/s10531-021-02271-y>.
- Oksanen, Jari, Gavin L. Simpson, F. Guillaume Blanchet, et al. 2025. *Vegan: Community Ecology Package*. V. 2.6-10. Released January 29. <https://cran.r-project.org/web/packages/vegan/index.html>.
- Pardee, Gabriella L., Kimberly M. Ballare, John L. Neff, et al. 2023. "Local and Landscape Factors Influence Plant-Pollinator Networks and Bee Foraging Behavior across an Urban Corridor." *Land* 12 (2): 2. <https://doi.org/10.3390/land12020362>.
- Pareek, Abhishek, B. M. Meena, Sitaram Sharma, M. L. Teterwal, R. K. Kalyan, and B. L. Meena. 2017. *Impact of Climate Change on Insect Pests and Their Management Strategies*.
- Patt, J. M., G. C. Hamilton, and J. H. Lashomb. 1997. "Impact of Strip-Insectary Intercropping with Flowers on Conservation Biological Control of the Colorado Potato Beetle." *Advances in Horticultural Science* 11 (4): 175–81.
- Pebesma, Edzer. 2018. "Simple Features for R: Standardized Support for Spatial Vector Data." *The R Journal* 10 (1): 439–46.
- Pebesma, Edzer, and Roger Bivand. 2023. *Spatial Data Science: With Applications in R*. Chapman and Hall/CRC. <https://doi.org/10.1201/9780429459016>.
- Peters, Marcell K., Andreas Hemp, Tim Appelhans, et al. 2019. "Climate–Land-Use Interactions Shape Tropical Mountain Biodiversity and Ecosystem Functions." *Nature* 568 (7750): 88–92. <https://doi.org/10.1038/s41586-019-1048-z>.
- Petit, Sandrine, Lucile Muneret, Benjamin Carbonne, et al. 2020. "Chapter One - Landscape-Scale Expansion of Agroecology to Enhance Natural Pest Control: A Systematic Review." In *Advances in Ecological Research*, edited by David A. Bohan and Adam J.

Vanbergen, vol. 63. *The Future of Agricultural Landscapes*, Part I. Academic Press.
<https://doi.org/10.1016/bs.aecr.2020.09.001>.

Pretty, Jules. 2018. “Intensification for Redesigned and Sustainable Agricultural Systems.” *Science* 362 (6417): eaav0294. <https://doi.org/10.1126/science.aav0294>.

“R: The Grid Graphics Package.” 2024. <https://stat.ethz.ch/R-manual/R-devel/library/grid/html/00Index.html>.

Rader, Romina, Ignasi Bartomeus, Lucas A. Garibaldi, et al. 2016. “Non-Bee Insects Are Important Contributors to Global Crop Pollination.” *Proceedings of the National Academy of Sciences* 113 (1): 146–51. <https://doi.org/10.1073/pnas.1517092112>.

Ragone, Gianvito, Ilaria Laterza, Biagio Tedone, et al. 2025. “Seminatural Habitats Support Both Grapevine Pests and Their Parasitoids in Mediterranean Organic Vineyards.” *Oecologia* 207 (January). <https://doi.org/10.1007/s00442-024-05661-5>.

Rand, Tatyana A., Jason M. Tylianakis, and Teja Tscharntke. 2006. “Spillover Edge Effects: The Dispersal of Agriculturally Subsidized Insect Natural Enemies into Adjacent Natural Habitats.” *Ecology Letters* 9 (5): 603–14. <https://doi.org/10.1111/j.1461-0248.2006.00911.x>.

Ries, Leslie, Robert Fletcher, James Battin, and Thomas Sisk. 2004. “Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained.” *Annual Review of Ecology and Systematics* 35 (December): 491–522.
<https://doi.org/10.1146/annurev.ecolsys.35.112202.130148>.

Rischen, Tamara, Matilda Kaffenberger, Eva Plath, Jessica Wolff, and Klaus Fischer. 2023. “Configurational Landscape Heterogeneity: Crop-Fallow Boundaries Enhance the Taxonomic Diversity of Carabid Beetles and Spiders.” *Agriculture, Ecosystems & Environment* 341 (January): 108194. <https://doi.org/10.1016/j.agee.2022.108194>.

Rosenzweig, Cynthia, Ana Iglesias, X. B. Yang, Paul R. Epstein, and Eric Chivian. 2001. “Climate Change and Extreme Weather Events; Implications for Food Production, Plant Diseases, and Pests.” *Global Change and Human Health* 2 (2): 90–104.
<https://doi.org/10.1023/A:1015086831467>.

Rusch, Adrien, Rebecca Chaplin-Kramer, Mary M. Gardiner, et al. 2016. “Agricultural Landscape Simplification Reduces Natural Pest Control: A Quantitative Synthesis.” *Agriculture, Ecosystems & Environment* 221 (April): 198–204. <https://doi.org/10.1016/j.agee.2016.01.039>.

Samaranayake, Kandanpita Galaddalage Lahiru Ishan, and Alejandro C. Costamagna. 2018. “Levels of Predator Movement between Crop and Neighboring Habitats Explain Pest Suppression in Soybean across a Gradient of Agricultural Landscape Complexity.” *Agriculture, Ecosystems & Environment* 259 (May): 135–46. <https://doi.org/10.1016/j.agee.2018.03.009>.

Schellhorn, N. A., F. J. J. A. Bianchi, and C. L. Hsu. 2014. “Movement of Entomophagous Arthropods in Agricultural Landscapes: Links to Pest Suppression.” *Annual Review of Entomology* 59 (Volume 59, 2014): 559–81. <https://doi.org/10.1146/annurev-ento-011613-161952>.

Schellhorn, Nancy A., Vesna Gagic, and Riccardo Bommarco. 2015. “Time Will Tell: Resource Continuity Bolsters Ecosystem Services.” *Trends in Ecology & Evolution* 30 (9): 524–30. <https://doi.org/10.1016/j.tree.2015.06.007>.

Shackelford, Gorm, Peter R. Steward, Tim G. Benton, et al. 2013. “Comparison of Pollinators and Natural Enemies: A Meta-Analysis of Landscape and Local Effects on Abundance and Richness in Crops.” *Biological Reviews of the Cambridge Philosophical Society* 88 (4): 1002–21. <https://doi.org/10.1111/brev.12040>.

Slowikowski, Kamil, Alicia Schep, Sean Hughes, et al. 2024. Ggrepel: Automatically Position Non-Overlapping Text Labels with “Ggplot2.” V. 0.9.6. Released September 7. <https://cran.r-project.org/web/packages/ggrepel/index.html>.

Tamburini, Giovanni, Giacomo Santoiemma, Megan E. O’Rourke, et al. 2020. “Species Traits Elucidate Crop Pest Response to Landscape Composition: A Global Analysis.” *Proceedings of the Royal Society B: Biological Sciences* 287 (1937): 20202116. <https://doi.org/10.1098/rspb.2020.2116>.

Thies, C., and T. Tscharntke. 1999. “Landscape Structure and Biological Control in Agroecosystems.” *Science (New York, N.Y.)* 285 (5429): 893–95. <https://doi.org/10.1126/science.285.5429.893>.

Thies, Carsten, Indra Roschewitz, and Teja Tscharntke. 2005. “The Landscape Context of Cereal Aphid–Parasitoid Interactions.” *Proceedings of the Royal Society B: Biological Sciences* 272 (1559): 203–10. <https://doi.org/10.1098/rspb.2004.2902>.

Thies, Carsten, Ingolf Steffan-Dewenter, and Teja Tscharntke. 2003. “Effects of Landscape Context on Herbivory and Parasitism at Different Spatial Scales.” *Oikos* 101 (1): 18–25. <https://doi.org/10.1034/j.1600-0706.2003.12567.x>.

Thuma, Jessie A., Genevieve Pugesek, Erin D. Treanore, Sylvana R. Finn, and Elizabeth E. Crone. 2025. “Bumble Bee Nest Density Is Lower in Drought Years.” *Proceedings. Biological Sciences* 292 (2056): 20251010. <https://doi.org/10.1098/rspb.2025.1010>.

Tortosa, Axelle, Brice Giffard, Clélia Sirami, Laurent Larrieu, Sylvie Ladet, and Aude Vialatte. 2023. “Increasing Landscape Heterogeneity as a Win–Win Solution to Manage Trade-Offs in Biological Control of Crop and Woodland Pests.” *Scientific Reports* 13 (1): 13573. <https://doi.org/10.1038/s41598-023-40473-2>.

Tscharntke, Teja, Daniel S. Karp, Rebecca Chaplin-Kramer, et al. 2016. “When Natural Habitat Fails to Enhance Biological Pest Control – Five Hypotheses.” *Biological Conservation* 204 (December): 449–58. <https://doi.org/10.1016/j.biocon.2016.10.001>.

Tscharntke, Teja, Alexandra M. Klein, Andreas Kruess, Ingolf Steffan-Dewenter, and Carsten Thies. 2005. “Landscape Perspectives on Agricultural Intensification and Biodiversity – Ecosystem Service Management.” *Ecology Letters* 8 (8): 857–74. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.

Tscharntke, Teja, Jason M. Tylianakis, Tatyana A. Rand, et al. 2012. “Landscape Moderation of Biodiversity Patterns and Processes - Eight Hypotheses.” *Biological Reviews of the Cambridge Philosophical Society* 87 (3): 661–85. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>.

Ugine, Todd A. 2012. “Developmental Times and Age-Specific Life Tables for *Lygus lineolaris* (Heteroptera: Miridae), Reared at Multiple Constant Temperatures.” *Environmental Entomology* 41 (1): 1–10. <https://doi.org/10.1603/EN10210>.

Vega, Sergio, Héctor Vázquez-Rivera, Étienne Normandin, Valérie Fournier, and Jean-Philippe Lessard. 2023. “Large Remaining Forest Habitat Patches Help Preserve Wild Bee Diversity in Cultivated Blueberry Bush.” *Diversity* 15 (3): 3. <https://doi.org/10.3390/d15030405>.

Veres, Andrea, Sandrine Petit, Cyrille Conord, and Claire Lavigne. 2013. “Does Landscape Composition Affect Pest Abundance and Their Control by Natural Enemies? A Review.” *Agriculture, Ecosystems & Environment, Landscape ecology and biodiversity in agricultural landscapes*, vol. 166 (February): 110–17. <https://doi.org/10.1016/j.agee.2011.05.027>.

Walker, Kyle. 2016. “Tigris: An R Package to Access and Work with Geographic Data from the US Census Bureau.” *The R Journal* 8 (2): 231–42.

Whipple, Sean D., Mathew L. Brust, Kerri M. Farnsworth-Hoback, and W. Wyatt Hoback. 2012. “Rangeland Grasshopper Numbers and Species Composition in Nebraska: A Comparison of Region and Sampling Location.” *Journal of Orthoptera Research* 21 (2): 269–77. <https://doi.org/10.1665/034.021.0213>.

Wickham, Hadley. 2016. *Ggplot2. Use R!* Springer International Publishing. <https://doi.org/10.1007/978-3-319-24277-4>.

Wickham, Hadley, Mara Averick, Jennifer Bryan, et al. 2019. “Welcome to the Tidyverse.” *Journal of Open Source Software* 4 (43): 1686. <https://doi.org/10.21105/joss.01686>.

Winters-Michaud, Clayton. 2024. *Major Uses of Land in the United States, 2017*. With Alfred Haro, Scott Callahan, and Daniel P. Bigelow. *Economic Information Bulletin / Economic Research Service ; Number 275*. United States Department of Agriculture, Economic Research Service. <https://doi.org/10.1133/8633522,%252010.32747/2024.8633522.ers>.

Yachi, Shigeo, and Michel Loreau. 1999. "Biodiversity and Ecosystem Productivity in a Fluctuating Environment: The Insurance Hypothesis." *Proceedings of the National Academy of Sciences* 96 (4): 1463–68. <https://doi.org/10.1073/pnas.96.4.1463>.

Zhang, Wei, Taylor H. Ricketts, Claire Kremen, Karen Carney, and Scott M. Swinton. 2007. "Ecosystem Services and Dis-Services to Agriculture." *Ecological Economics, Special Section - Ecosystem Services and Agriculture*, vol. 64 (2): 253–60. <https://doi.org/10.1016/j.ecolecon.2007.02.024>.

Zhu, Hui, Xuehui Zou, Deli Wang, Shiqiang Wan, Ling Wang, and Jixun Guo. 2015. "Responses of Community-Level Plant-Insect Interactions to Climate Warming in a Meadow Steppe." *Scientific Reports* 5 (1): 18654. <https://doi.org/10.1038/srep18654>.

Zilnik, Gabriel, Paul E. Bergeron, Angela Chuang, et al. 2023. "Meta-Analysis of Herbicide Non-Target Effects on Pest Natural Enemies." *Insects* 14 (10): 787. <https://doi.org/10.3390/insects14100787>.

Zwaan, Devin R. de, Kevin C. Hannah, Niloofar Alavi, et al. 2024. "Local and Regional-Scale Effects of Hedgerows on Grassland- and Forest-Associated Bird Populations within Agroecosystems." *Ecological Applications* 34 (3): e2959. <https://doi.org/10.1002/eap.2959>.

Chapter 3 - Climate and human-modified landscapes influence spread of invasive agricultural pest *Popillia japonica* Newman in American Midwest and Great Plains

Published as: Kuchеров, N.B., Hefley, T. & Kim, T.N. Climate and human-modified landscapes influence spread of invasive agricultural pest *Popillia japonica* Newman in American Midwest and Great Plains. *Sci Rep* **15**, 33013 (2025). <https://doi.org/10.1038/s41598-025-18493-x>

Abstract

Japanese beetle (*Popillia japonica*) is an invasive agricultural pest throughout the eastern United States and its distribution is expanding westward. Understanding how climate and land use intensification interact to affect Japanese beetle population dynamics and spread is essential to predict which areas are vulnerable to increased pest pressure. In this study, we combine data from the Global Biodiversity Information Facility (GBIF) with data from local state agricultural agencies and University extension offices to model how land cover and climate affect Japanese beetle occurrences at the leading edge of an invasion front in the central United States over 5 years. We found that beetle occurrences were positively correlated with proportion of developed areas, proportion of corn and soybean, minimum temperature, and precipitation within counties, and negatively correlated with the proportion of grassland and pasture, and maximum temperature. We modeled Japanese beetle occurrences in the near future and for future climate scenarios and found high probability of occurrence for Japanese beetles across the entire region. Our study highlights the importance of supplementing community science data in rural areas and including a time variable when assessing habitat associations for invasive species in novel areas.

Introduction

Changing environments, caused by climate and land cover change, are negatively affecting pest dynamics in agroecosystems and threatening food security. To meet growing demands for food, global agricultural production must double by 2050, and the suggested way is to intensify crop yield production rather than expand agricultural land (Tilman et al. 2011).

However, agricultural intensification has led to increased pesticide usage with negative effects on non-target species such as wildlife and beneficial insects (Thurman et al. 2017), harm to human health (Elahi et al. 2019), and increased insecticide resistance (Khodaverdi et al. 2016, Hough et al. 2017). These outcomes are exacerbated with changes in temperature and weather patterns which will affect insect life cycles, survivability, and pest outbreaks (Thomson et al. 2010, Jactel et al. 2012, Eigenbrode et al. 2015, Skendžić et al. 2021), as well as relationships between pests and their natural enemies (Prakash et al. 2014, Thurman et al. 2017, Urbaneja-Bernat et al. 2019). Invasive species are particularly problematic, causing a reduction in food supply with global costs of \$279 billion USD in 2019 (Roy et al. 2024), and their impact is expected to rise with increased global trade (Paini et al. 2016) and climate change (Skendžić et al. 2021). Therefore, understanding how climate and land use intensification interact to affect invasive pest population dynamics and spread is essential for effective and targeted management efforts.

One invasive pest that is of major concern in the United States is the Japanese beetle (*Popillia japonica* Newman). Japanese beetles feed on over 300 plant species, including turfgrass, horticultural plants, fruit crops, soybean, corn, and other field crops (Fleming 1972, Potter and Held 2002, Shanovich et al. 2019). Native to Japan, Japanese beetles were introduced to the United States in 1916 through a nursery in New Jersey (Dickerson and Weiss 1918, Smith and Hadley 1926) and by 1998, they quickly spread to all states east of the Mississippi river, except Florida (Kistner-Thomas 2019). As of 2015, there were established populations in 28 eastern states and moderate populations in states west of the Mississippi River (Kistner-Thomas 2019). Japanese beetles have recently become a growing concern for the Midwestern United States, due to their potential to damage corn and soybean production (Shanovich et al. 2019).

Japanese beetles defoliate soybean plants, causing severe damage if they defoliate the leaves during a reproductive stage (e.g., approximately 20% yield loss after 30% defoliation (Hammond 1994)). In corn, Japanese beetles clip the silks, which interferes with pollination, causing a reduction of kernels (Edwards 1999). The economic impact of Japanese beetles in the United States was estimated as \$450 million per year by ARS in 2010 (Flores 2010). However, it is likely to be far higher now. A recent report estimated economic damage by the Japanese beetle in Utah would be \$126 million in 2027 (Grundon and Schmucker 2020). Even with current controls and quarantines, Japanese beetle expansion continues to threaten agriculture and horticulture as they move westward in the United States.

Investigating how invasive species, such as the Japanese beetle, expand their distribution is challenging for many reasons (Liu et al. 2020). Current models studying the expansion of Japanese beetle rely on occurrence data from different regions to determine habitat associations within a novel region which can be problematic especially along invasion fronts such as the Midwestern US (Kistner-Thomas 2019, Della Rocca and Milanesi 2022a, Borner et al. 2023). For example, Zhu et al. (2017) found that habitat association models using Japanese beetle occurrence, climate and land cover data from the native range in Japan was not able to explain Japanese beetle distribution within the introduced range in North America. This discrepancy could arise because invasive species within a novel habitat have not filled their ecological niche, and therefore absences could simply be due to not having enough time to reach unoccupied areas rather than negative associations (Elith et al. 2010). As such, habitat associations within the native range (where all ecological niches have been occupied) can be different from the associations within the non-native range (Wiersma et al. 2011). Additionally, the spatial extent can affect habitat associations as climate factors may better correlate with species occurrences at

a global scale due to greater variability in climate at larger spatial scales, while environmental factors may better explain the occurrence of species at finer scales due to greater variability at these smaller spatial scales (Elith and Leathwick 2009). Therefore, to improve our understanding of how Japanese beetles utilize landscapes and predict their regional occurrences in the future, we need to create habitat association models at the appropriate spatial extent and location by incorporating regional environmental, climatic, and anthropogenic factors.

Another challenge for understanding habitat associations is the quality of the occurrence data used to create the statistical model. Invasive species present unique spatial biases because eradication efforts can obscure natural habitat associations, sampling protocols can differ across political boundaries, and sampling efforts may vary in the long-establish versus the recently invaded areas (Lake et al. 2020). Additionally, studies that pool all occurrence observations together as one point in time and then predict the distribution for a future time or climate scenarios (Kistner-Thomas 2019, Della Rocca and Milanesi 2022a, Borner et al. 2022) can be problematic because this approach assumes that the population of the modelled species is currently in equilibrium with its environment (Menke et al. 2009, Elith et al. 2010). When modeling invasive species, habitat associations can be obscured simply because the invasive species has not yet spread to a given location (Lodge et al. 2016). Sampling bias is also introduced when using community science data which allows data to be collected across large geographical areas and over a long period of time (Hughes et al. 2024). These sampling biases include missing data which might confound data gaps in unsampled areas from true absences (Bowler et al. 2024) and variation in observation effort with more observations occurring in populated areas and incomplete detection in less populated areas (Altwegg and Nichols 2019). Due to the nature of community science, observations are collected in areas where users spend

their time, while large expanses of private property are not explored, leading to the underrepresentation of agricultural and rural areas. Therefore, biased occurrence data could be misleading in understanding habitat associations, and an effort must be made to incorporate data from other sources.

For this study, we examine habitat associations of Japanese beetles, *Popillia japonica*, and predict their occurrences along the invasion front within the Great Plains and Midwest regions of the United States. We address the challenges outlined above to model habitat associations of Japanese beetles in the states of Iowa, Kansas, Missouri, and Nebraska, United States, over a five-year period (2017 - 2021). By using data from this time and spatial range, we can capture how Japanese beetles are utilizing landscapes at the leading edge of an invasion front and predict future spread. We use community science occurrence data from the Global Biodiversity Information Facility, GBIF (www.gbif.org), along with presence-absence data from state agricultural agencies and University extension offices to overcome spatial biases associated with public databases. This study is the first to combine two such datasets to analyze the effects of land cover and climate variables on the spread of the Japanese beetle in a novel area. The addition of observation data from state agricultural agencies and extension offices is integral to understanding how this invasive agricultural pest spreads in an agriculturally dominated landscape such as the American Midwest. We hypothesized that Japanese beetle presence will have a positive relationship with developed areas, as well as grasslands and pasture, and agricultural land due to availability of food resources. We also hypothesized a positive relationship between Japanese beetle presence and precipitation, as these beetles prefer warmer temperatures and moist soil (Fleming 1972, Potter and Held 2002). We hypothesized that lower precipitation would result in lower probabilities for Japanese beetle presence in the western

portion of this region, especially under possible future drier climatic conditions. We then used our habitat association model to understand and predict how Japanese beetles are spreading into novel areas of this region. This knowledge could be used to guide mitigation efforts of the beetle and minimize its impact on important agricultural production in the central United States.

Methods

Study Area

For this study, the four states of Iowa, Kansas, Missouri, and Nebraska were chosen due to their location along the western invasion front of the Japanese beetle in the United States (Fig. 1). Assuming that an invasive species will have the same habitat associations across its entire range can lead to false predictions (Wiersma et al. 2011), therefore here we focus on habitat associations within this region to better infer relationships between the spread of Japanese beetles and regional landscape and climate factors. According to recent models, the climate-suitable range of Japanese beetles within the United States remains partially unfilled, and some un-infested areas are at risk for invasion now, under current climate conditions (Zhu et al. 2017). Additionally, there is concern that the managed pastures of this region will provide ideal habitat for Japanese beetle larvae (Kistner-Thomas 2019). In the four years between 2018 and 2022, Nebraska's infestation status changed from partially infested to generally infested, indicating an advancing western invasion into the Great Plains (Fig. 1).

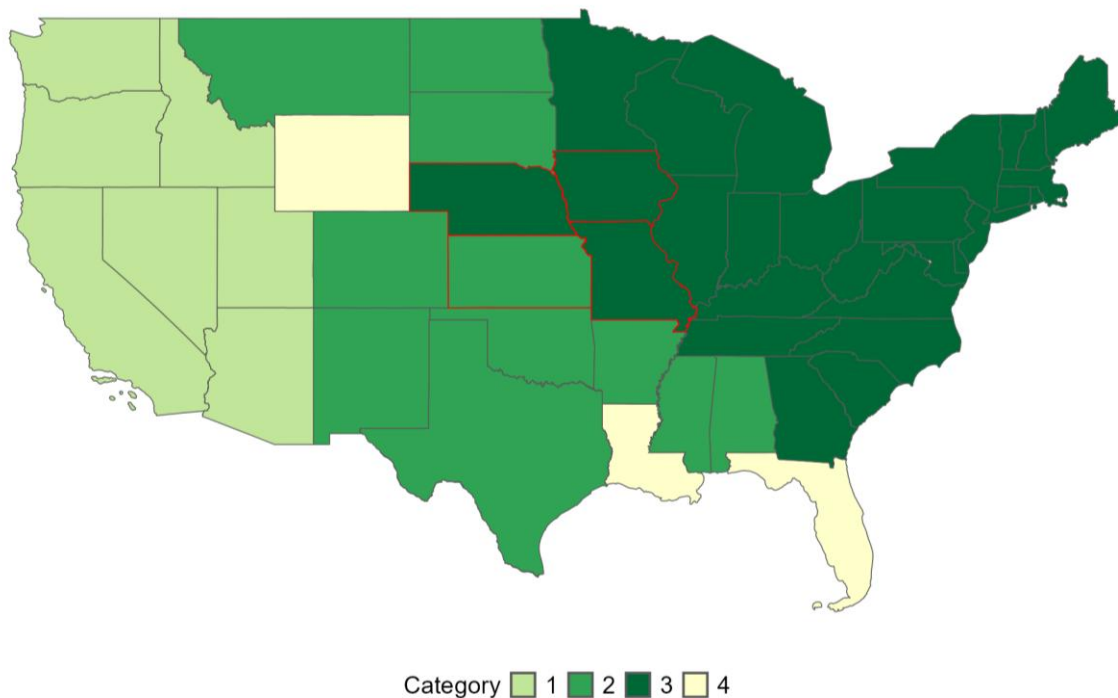


Figure 3-1 United States map of Japanese beetle (Jb) infestation status by state. States listed as “Category 1” are uninfested and Jb are considered quarantined pests. “Category 2” are uninfested or partially infested states and Jb are regulated but not quarantined. “Category 3” are partially or generally infested state, and Jb are not regulated. “Category 4” states are not known to be infested. (modified from Japanese Beetle Harmonization Plan, 2022)

Data collection

We obtained occurrence data on Japanese beetle observations from Global Biodiversity Information Facility, GBIF(GBIF.org n.d.). Data were downloaded using a structured search for all entries of the species “*Popillia japonica* Newman, 1838” entered as a human observation within the United States and including coordinates. This search led to 16,493 observations(GBIF.org n.d.). Observations which did not include data on “State/province” were omitted. We filtered the GBIF observations down to the four states (Iowa, Nebraska, Missouri, and Kansas) and years (2017 - 2021) of our study, resulting in 1141 observations. There were only 39 observations within these states prior to 2017.

We gathered our supplementary data from state agricultural sources through presence/absence county maps provided online and personal correspondence. The state data from Iowa was compiled through reports of Japanese beetle sightings from landowners and extension officials and retrieved through personal correspondence (D. Lewis, personal communication, 29 Jan 2024). In Nebraska and Kansas, the state's Department of Agriculture is actively monitoring and trapping Japanese beetles. For Nebraska, we used the presence/absence county maps provided online by the Department of Agriculture (Nebraska Department of Agriculture n.d.). For Kansas, we obtained trapping data from the Department of Agriculture (R. Wilkins, personal communication, 29 Apr 2024). For Missouri, we received trapping data from a monitoring effort based at University of Missouri (K. Rice, personal communication, 9 Nov 2022).

Land cover data were downloaded by county from USDA's Cropland data layer (CDL) (USDA National Agricultural Statistics Service 2022) using the CropscapeR package (Chen 2020). For each county, we calculated the percentage of land cover that was designated as corn, soybean, grassland and pasture, and developed areas. The developed land cover variable is the sum of the low, medium, and high intensity, as well as developed open space areas because they all represent human-dominated landscapes where lawns and turf would be present. County level climate variables for average annual temperature, annual maximum temperature, annual minimum temperature, and total annual precipitation between 2017 - 2021 were downloaded from NOAA's Climate at a Glance County Time Series (NOAA National Centers for Environmental Information 2023).

Data conversion

To help counter the community science bias towards developed and populated areas, we combined the filtered data from our GBIF occurrence download(GBIF.org n.d.) for each year with the annual data from agricultural agencies in each of the four states, matching the data temporally. Because we used different data sources which were not sampled in the same manner, we looked at occurrences within counties rather than abundance(Woodcock et al. 2016). For the GBIF data, we converted presence point data to county level occurrence. Using R, version 4.2.1(R Core Team 2022), we layered latitude and longitude coordinates from the GBIF observations and trap locations for each year (2017 - 2021) onto the county geographies from the tigris package(Walker 2016, 2024) to convert our point data into county data.

The state data sets were individually transformed to county presence/absence as follows. For Nebraska counties, we considered the county map data as true presences or absences as they were actively trapping for Japanese beetles in all counties. In Kansas, active monitoring is also occurring, but not in every county as the Japanese beetle has not spread through much of western Kansas. For Kansas counties, it was considered an absence if there were either zero Japanese beetles in their traps or trapping was not occurring. However, in Iowa where the maps are made based solely on reports of Japanese beetle presence, we treated the counties with no Japanese beetle sightings reported as “NA”. For Missouri, we our trapping data did not include all counties, so counties with zero Japanese beetles in their traps were treated as true absences while counties without traps set out were left as “NA”.

To create our final data set, we combined the county level GBIF and state datasets described above. The four states (Iowa, Nebraska, Missouri, and Kansas) had a total of 412 counties, and each county was marked with whether Japanese beetle was present in either of the data sources (GBIF or state) or absent from both of them each year for five years (2017 - 2021). If a county was marked as “NA” in the state dataset and did not have a GBIF sighting, then we could not differentiate true absences from under sampling in that county (i.e., “unknown” data). These counties (12% of the observations) were left as “NA” in the dataset and omitted from the model training data and model testing calculations.

Generalized additive models

We created generalized additive models (GAMs) to examine the effects of land cover type (corn and soybeans, grassland and pasture, developed areas), climate (average temperature, maximum temperature, minimum temperature, precipitation), state (Nebraska, Iowa, Missouri, and Kansas), and year (2017, 2018, 2019, 2020, 2021) on Japanese beetle presence/absence using the *mgcv* package (Wood 2011, 2017). The variable of state was included to control for administrative differences within these political boundaries (Lake et al. 2020), as the status of Japanese beetle infestation, as well as the monitoring of Japanese beetles varies across the four states. We tested for multicollinearity using the variance inflation factor (VIF) function from the package *car* (Fox and Weisberg 2019). The average temperature variable had a very high VIF (>300), and its effect was similar to the minimum temperature variable. Since minimum temperatures may indicate inhospitable areas due to the lower thermal limits of overwintering Japanese beetle larvae (Potter and Held 2002, Shanovich et al. 2019), we removed average temperature from our models.

We fit generalized additive models using binomial distributions with a logit link function. We performed model selection starting with our full hypothesis model, which included all of our predictor variables: county-level proportion of corn and soybean (ranging from < 0.001 to 0.886), grassland and pasture (ranging from 0.005 to 0.978), and developed areas (ranging from 0.002 to 0.928), maximum temperature (ranging from 11.278 to 22.389), minimum temperature (ranging from -0.667 to 10.778), precipitation (ranging from 221.7 mm to 1794.7 mm), state (Nebraska, Iowa, Missouri, and Kansas), and year (2017, 2018, 2019, 2020, 2021). We compared our full model to simpler versions, removing variables at each step. We confirmed that all the variables we chose added value over the simpler options using AIC comparisons to find the strongest model (Burnham et al. 2011). The strongest model was the model with the lowest AIC score, however if models were within 2 delta AIC of one another, the simpler model was chosen.

Model validation was performed by using the 2017 - 2020 data as a training set and holding back the 2021 data as a test set. We compared the 2021 model predictions with the actual 2021 occurrences, and we measured the accuracy of the models using Zero-One scoring (Gneiting and Raftery 2007).

Forecasting data

We used the model with the lowest AIC to predict the spread of Japanese beetles in two ways: (1) into the near future (2025 and 2030) under current climate conditions, and (2) using future climate scenarios (RCP 2.6 and RCP 8.5), as described in the Physical Science Basis report of the Intergovernmental Panel on Climate Change (Climate change 2013 2013). First, we model our data forward in time ~ 5 years and ~ 10 years to visualize the spread of Japanese

beetles under current climate conditions. To build the predictive dataset, we used 5-year averages (2017 - 2021) of land cover and climate data to represent the current climate and land cover conditions. We used the most recent 5-year averages versus 30-year climate normal because the biology and spread of Japanese beetle is more likely to be affected by current climate conditions. We changed the year variable in our predictive dataset to project the Japanese beetle spread forward in time. For future climate scenarios, we used the year 2030 to account for realistic further spread. We forecasted two different climate scenarios based on a better-case scenario for climate change and a worst-case scenario (Climate change 2013 2013). For both future climate scenarios, we kept the land cover data as current five year averages (2017 – 2021). The first scenario is based on RCP 2.6; for this we adjusted our 5-year average dataset with a one-degree Celsius temperature increase and a ten percent increase in precipitation (Climate change 2013 2013). The second scenario is based on RCP 8.5; for this we adjusted our 5-year average dataset with a four-degree Celsius increase in temperature and a ten percent decrease in precipitation (Climate change 2013 2013). Unfortunately, predictive intervals are not available for GAMs, so we were not able to estimate them (Wood 2017).

Results

Model performance and validation

The model with the lowest AIC score included developed areas, corn and soybean, grassland and pasture, precipitation, minimum temperature, maximum temperature, state and year. With Zero-One scoring, our model, trained with 2017 - 2020 data, had an accurate prediction rate of 90.6% and correctly predicted the status of 326 of the 360 counties in 2021 (Fig. 2). The model was better at predicting true positives (94.9%) than true negatives (80.3%).

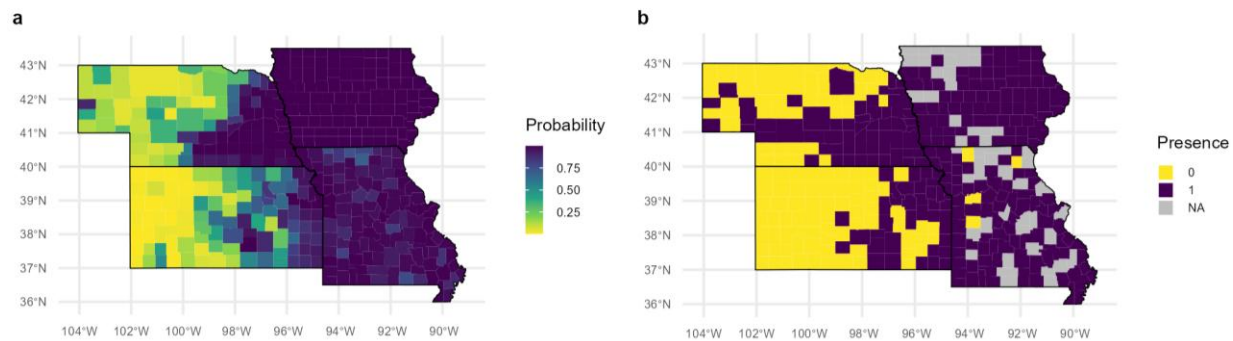


Figure 3-2 Comparison of the model prediction values for Japanese beetle presence for 2021 (a) with the actual presence values in 2021 at the county levels (b). For actual presence values, 1 indicates that Japanese beetles were present in the county, 0 indicates that they were absent, and NA indicates that the status was unreported to both data sources.

Relationships with predictor variables

For land cover variables, there were significant relationships between Japanese beetle presence and developed areas, corn and soybean, and grassland and pasture (Table 1). Developed areas had a very strong positive relationship with Japanese beetle presence, with high probability of presence reached with even a small proportion (0.10) of developed areas ($p < 0.001$, Fig. 3a). Agricultural land planted with corn and soybean had a significant positive relationship with Japanese beetle presence ($p < 0.05$, Fig 3b). Finally, there was a significant negative relationship between Japanese beetle presence and grassland and pasture ($p < 0.01$, Fig 3c).

Table 3-1 Model relationships between Japanese beetle occurrences and climate and land cover variables ($r^2 = 0.692$).

Predictive Variable	edf	Ref.df	Chi sq.	<i>P</i>
Developed Areas	3.704	4.304	62.29	<0.001

Corn and Soybean	7.195	8.136	19.28	<0.05
Grassland and Pasture	8.688	8.959	26.67	<0.01
Maximum Temperature	2.898	3.665	15.20	<0.01
Minimum Temperature	4.205	5.309	12.78	<0.05
Precipitation	6.440	7.591	20.52	<0.05

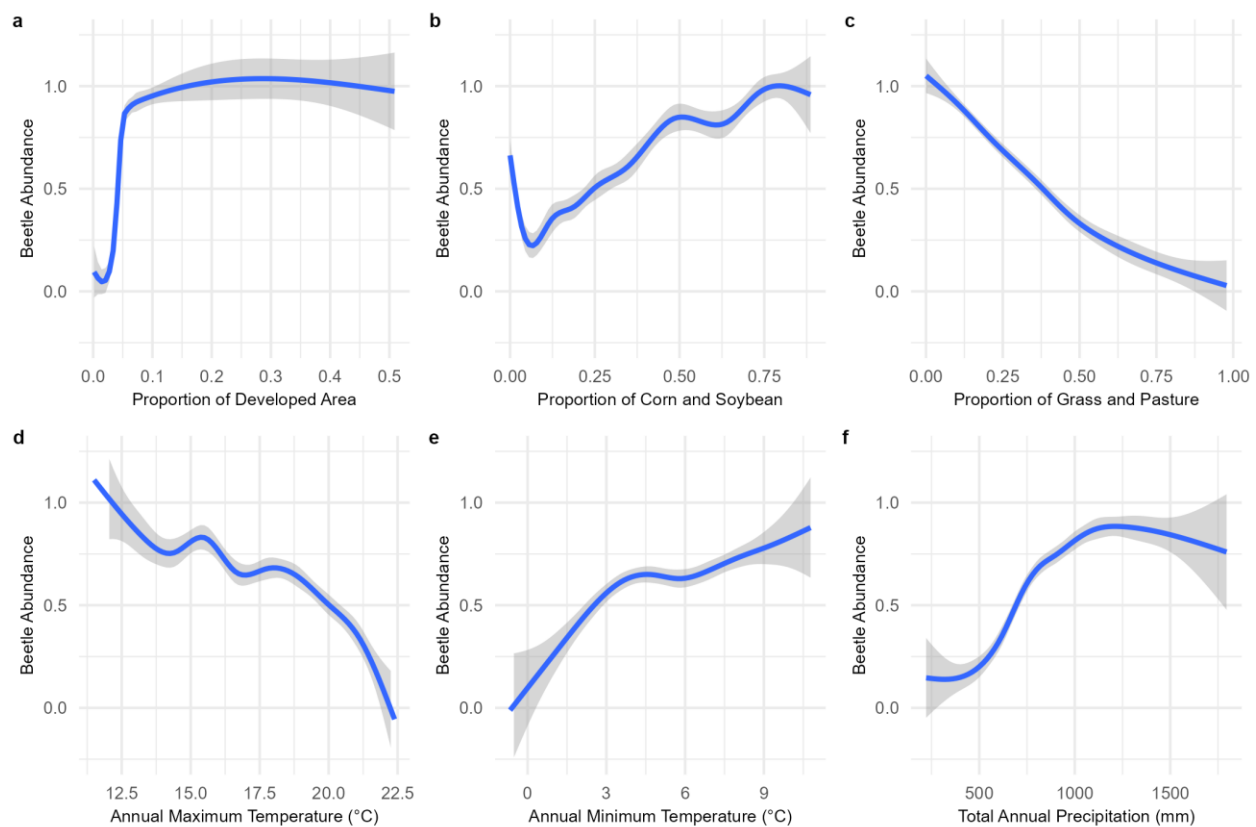


Figure 3-3 Relationships between each land cover and climate variable and Japanese beetle presence/absence shown with a smooth line. The grey shading represents the 95% confidence intervals. The probability of use varies with proportion of developed areas (a), proportion of corn and soybean (b), proportion of grassland and pasture (c), annual mean maximum temperature in degrees Celsius (d), annual mean minimum temperature in degrees Celsius (e), and total annual precipitation in mm (f).

For climate variables, maximum temperature, minimum temperature and precipitation were also all significant. Maximum temperature had a significant negative relationship with Japanese beetle presence ($p < 0.01$, Fig 3d). Japanese beetle presence increased steadily as minimum temperature increased ($p < 0.05$, Fig. 3e). Precipitation had a significant positive relationship with Japanese beetles which plateaued around 1000 mm of annual precipitation ($p < 0.05$, Fig. 3f). There were also significant relationships with the state and year variables, indicating the importance of time and space (Table 2).

Table 3-2 Model relationships between Japanese beetle occurrences and state and year ($r^2 = 0.692$).

Coefficient	Estimate	Std. Error	z value	Pr(> z)
Intercept (Kansas)	1298.000	233.700	-5.555	<0.001
Iowa	63.660	3.961 e^06	0.000	0.999
Missouri	1.062	0.368	2.889	<0.01
Nebraska	3.135	0.572	5.484	<0.001
Year	0.643	0.116	5.556	<0.001

Model predictions

We modeled the expansion of the Japanese beetle invasion in two ways. First, we used average climate conditions over the last 5 years to predict spread over the next few years (2025 and 2030). Using this approach, we found that Japanese beetles will likely spread out from the current infested counties, beyond the areas predicted from previous models (Kistner-Thomas 2019, Borner et al. 2022) and into the western areas of Nebraska and Kansas (Fig. 4a). Nebraska is predicted to be more suitable than Kansas, with southwestern Kansas having the lowest suitability (0 - 0.25), even into 2030 (Fig. 4b).

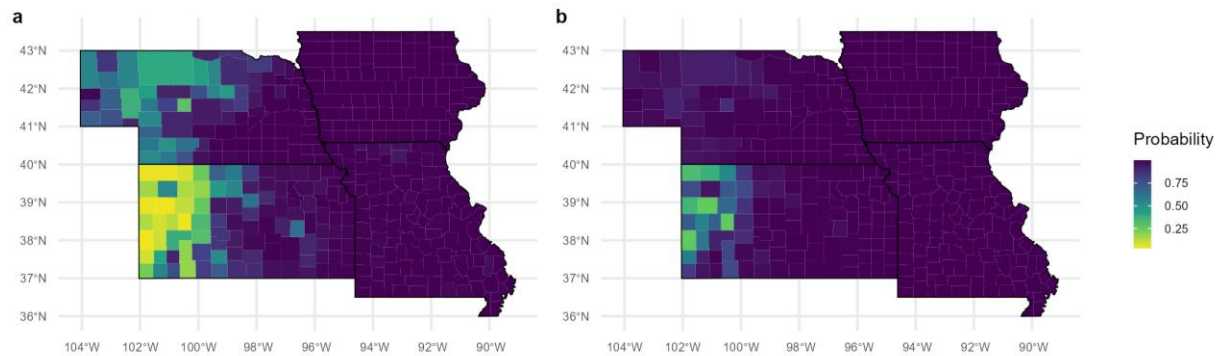


Figure 3-4 GAM predictions for Japanese beetle suitability per county for 2025 (a) and 2030 (b) under average climate and land cover conditions for 2017 - 2021.

Next, we modeled Japanese expansion under future climate scenarios. Our predictions for Japanese beetle presence under an RCP 2.6 climate scenario (a one-degree Celsius increase and ten-percent precipitation increase) suggest that a similar area will be suitable to Japanese beetles as under current climate conditions, but the increase in precipitation in the western region will slightly increase its suitability (Fig. 5a). Our predictions for Japanese beetle presence under an RCP 8.5 climate scenario (a four-degree Celsius increase and ten-percent precipitation decrease) suggest a range compression, mainly in the southwestern area of the region due to the combined hotter and drier climate (Fig. 5b).

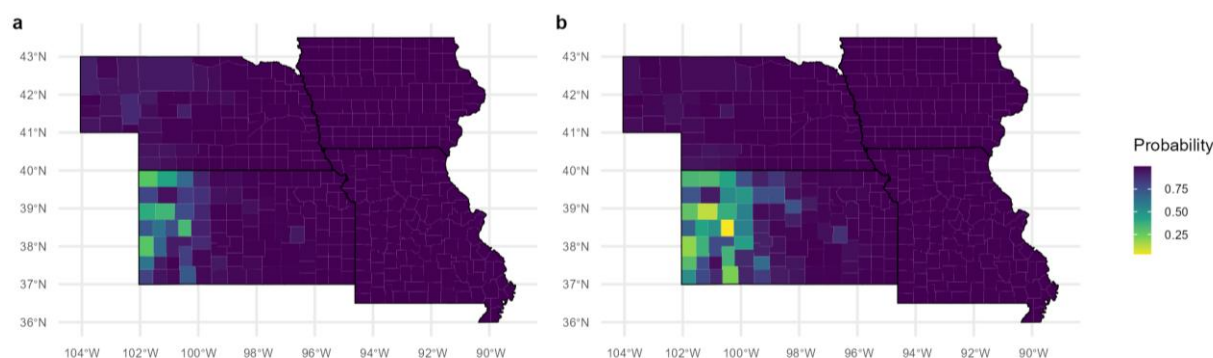


Figure 3-5 GAM predictions for Japanese beetle suitability per county under future climate scenarios, for the RCP 2.6 scenario with a temperature increase of 1°C and a 10% increase in precipitation (a) and the RCP 8.5 scenario with a temperature increase of 4°C and a 10% decrease in precipitation (b) and average land cover conditions for 2017 - 2021.

Discussion

The main objectives of this study were to infer regional habitat associations for the Japanese beetle in the American Midwest and Great Plains, and to predict the future spread of the Japanese beetle, specific to this region. We used yearly presence and absence observations of the Japanese beetle over a 5-year period of diffusion at the leading edge to guide our inference and predictions. We identified habitat associations with developed areas, agricultural land planted with corn and soybean, and grassland and pasture, as well as associations with key climatic variables; minimum and maximum temperature and precipitation (Fig. 3). Our model predictions indicate a higher probability of Japanese beetle infestations in this area than previously estimated (Kistner-Thomas 2019, Della Rocca and Milanesi 2022a), with only slight changes under future climate scenarios. This difference could be due to differences in the temporal and spatial extents of our study and the use of county and extension data to supplement community science data. We discuss these issues in greater detail below.

We found that all land cover variables, the percentage of developed areas, corn and soybean, and grassland and pasture, had significant relationships with Japanese beetle presence. As expected, developed areas had strong significant positive relationship with Japanese beetle presence. Counties with 10% or more developed area are highly likely to have Japanese beetles (Fig 3a). Sharp increases in the probability of Japanese beetle infestation, even at low levels of developed areas, could be due to the fact that these developed areas provide important habitat for the development of Japanese beetle larvae, such as turfgrass (Fleming 1972, Potter and Held 2002). Additionally, Japanese beetles are known to hitchhike into new regions on planes, trains, and automobiles in a form of unintentional human-mediated transport (Borner et al. 2024). Higher proportions of developed areas also indicate more populated counties with higher possibilities for human mediated dispersal.

The amount of corn and soybean also had the expected significant positive relationship with beetle presence (Fig. 3b). This supports our hypothesis based on Japanese beetle biology, as adults feed on field crops such as soybean and corn, and they have also been found to oviposit in field crops, with a preference for soybean and no-till fields (Shanovich et al. 2019). Japanese beetles use resources from both developed areas and agricultural fields throughout their life cycle. Previous studies have found that interactions between agriculture and other areas are especially important for Japanese beetles. Della Roca (2022b) found that Japanese beetles were more likely to occupy areas with not only a large amount of agriculture, but which also provided high habitat diversity. Borner et al. (2022) also cited the availability of multiple food sources as an explanation for why broad-leaved forests in proximity to open space were the most relevant

land-use variable. A mixture of agricultural and developed land cover types could benefit Japanese beetles because they use resources from both at different points in their life history. Although as adults Japanese beetles are considered a generalist species with over 300 host plants (Fleming 1972, Potter and Held 2002, Shanovich et al. 2019), females show a preference for specific oviposition conditions, such as short grass cover (Hawley 1944, Potter and Held 2002) and moist soils (Potter et al. 1996, Potter and Held 2002), and larval diet consists mainly of grass roots (Fleming 1972, Potter and Held 2002, Shanovich et al. 2019, Althoff and Rice 2022). Agricultural areas near developed areas with turfgrass and other larval habitat are likely the most at risk for Japanese beetle infestation.

However, we found a negative relationship between the probability of Japanese beetle presence and the amount of grassland and pasture in the county (Fig. 3c). This was unexpected as grass roots are the primary diet of Japanese beetle larvae (Fleming 1972, Potter and Held 2002, Shanovich et al. 2019) and it was predicted that managed pastures would allow Japanese beetles to thrive in areas of the central United States where it would otherwise be too dry (Kistner-Thomas 2019). Japanese beetles might consider grasslands of the Midwest as an undesirable natural area, despite prior research that females deposit their eggs in grass and pasture (Fleming 1972, Shanovich et al. 2019). Although this is the opposite of what we would expect based on established Japanese beetle populations in the eastern United States (Fleming 1972), a recent study in northern Italy also found that the probability of Japanese beetle presence decreased with higher percentages of pastures (Della Rocca and Milanese 2022b). This could be due to the variation in grassland composition across these different regions. For example, there are 65 distinct types of grasslands across the world all classified as “grassland” (Dixon et al. 2014).

Grasslands have distinctive characteristics, such as grass species, soil moisture, height, and management practices. Tallgrass prairies of the Midwest and Great Plains have characteristically tall, dense, stands of grass with deep root systems (Weaver and Fitzpatrick 1932). These root systems may be problematic for grubs that feed on grass roots and move up and down in the soil profile from fall to spring. It could also be due, in part, to an increase in predators of the Japanese beetle, such as grassland birds (Fleming 1968).

Unfortunately, recent demand for sustainable fuels have increased cropland for corn and soybean in the Midwest (Zhang et al. 2021) with the majority of the land coming from converting grasslands which were previously Conservation Reserve Program (CRP) land and pasture (Morefield et al. 2016, Lark et al. 2020). A study looking urbanization across the United States found that impervious surface area also increased by around 11% over a decade, and that the impervious surface area per person was highest in the Midwest (Bounoua et al. 2018). While we did not model how land cover change scenarios would affect the distribution of the Japanese beetles, the future expansion of cropland or urbanization at the expense of grassland could expedite the expansion of the Japanese beetle's range. Based on the negative association of grasslands and Japanese beetle occurrence in our model, the conservation of native grasslands could be helpful in slowing the spread of Japanese beetles.

Temperature and precipitation are known to affect Japanese beetle, and in our model, maximum temperature, minimum temperature, and precipitation had significant relationships with Japanese beetle presence (Table 1). From our analysis, we can see that maximum temperature has a negative relationship with beetle presence (Fig. 3d). While warmer temperatures are conducive to Japanese beetle population growth, higher maximum temperatures

could have a negative effect on Japanese beetles, as beetle eggs will not hatch above 34°C (Fleming 1972) and decreased numbers of Japanese beetles in Arkansas were attributed to hotter summers (Petty et al. 2015). Niziolek et al. (2013) found that Japanese beetles consumed more leaf matter in higher temperatures, but those that fed at elevated temperatures also exhibited increased mortality, especially above 37°C. Our results also indicate a significant positive relationship with minimum temperature (Fig. 3e). Minimum temperature corresponds to the lower thermal limit at which the larvae can survive, and areas with extremely cold winters are inhospitable to Japanese beetles as their supercooling point is -7°C (Potter and Held 2002). Therefore, higher minimum temperatures are likely to lead to greater survival of Japanese beetle larvae. Our model shows a generally positive relationship between precipitation and the probability of beetle presence, but the positive relationship plateaus at around 1000 mm (Fig 3f). While lower precipitation can deter Japanese beetle presence, our models show that under the current climate conditions, even most drier portions of western Kansas are likely to have Japanese beetles with the passing of time. This may be because although Japanese beetles are known to oviposit in soils with a moderate to high moisture content, it is only the eggs and first instars which are sensitive to desiccation (Fleming 1972, Allsopp et al. 1992). Therefore, areas with higher moisture such as lawns and irrigated crop fields could provide adequate habitat even during times of drought (Potter and Held 2002, Kistner-Thomas 2019).

For future predictions, our results show that Japanese beetles will quickly spread across the American Midwest and Great Plains. Although previous models based on global occurrences of Japanese beetles have shown lower suitability for a large portion of the western area of our

study region (Kistner-Thomas 2019, Della Rocca and Milanesi 2022a, Borner et al. 2022), our model suggests that this area is more suitable than previously thought.

Given the conflicting relationships with minimum and maximum temperature, we would expect global temperature increases to expedite the spread of Japanese beetles only up to a certain point. The increase of temperature minimums would decrease losses of Japanese beetle eggs or larvae in the cooler months. However, an increase in maximum temperature could cause mortality in the summer months. Changes in precipitation can also affect Japanese beetle, with increased precipitation favoring quicker expansion and greater abundance. Low precipitation has long been predicted as a barrier to Japanese beetle infestation west of the 100th meridian (Fleming 1972) and a decrease in precipitation could slow the spread of Japanese beetles to that area. Indeed, when we forecasted for the presence of Japanese beetles under two climate scenarios (RCP 2.6 and RCP 8.5), our model concurred with these expectations. In an RCP 2.6 scenario, with an increase in temperature as well as precipitation, the probability for Japanese beetle presence increased in the western areas of this region (Fig. 5a). However, with the RCP 8.5 scenario, which included an even higher temperature increase but a precipitation decrease, our models suggest that the southwestern portion will become less hospitable to Japanese beetles (Fig. 5b). Our climate predictions are similar to predictions by Kistner-Thomas (2019) which also show a northeastern range-shift for suitability under the RCP8.5 scenario and diverge from predictions by Della Rocca and Milanesi (2022) which show high suitability for this entire region under future climate scenarios. Our model's future climate predictions are in-line with observed effects of increased temperature on Japanese beetle mortality in experimental settings (Niziolek et al. 2013) and abundance in field settings (Petty et al. 2015).

Differences between our model predictions and previously published predictions (Kistner-Thomas 2019, Della Rocca and Milanese 2022a, Borner et al. 2022) could be due in part to the rural composition in these areas, as we used state agency and University extension data to supplement the GBIF data which increased Japanese beetles occurrence within the counties by more than two-fold. Without this addition of these data from rural and agricultural areas, relationships with land cover and climate variables could be missed, especially along this invasion front. The differences between our models and previous global models could also be due to differences in the temporal and spatial extents of the models. Habitat associations can vary by region (Menke et al. 2009, Davis et al. 2014) and these associations can be obscured if models are created at a much broader spatial scale such as global models (Elith and Leathwick 2009). On the other hand, if a spatial extent is too small, habitat associations can be clouded by differences in sampling and management efforts across political boundaries. In our model, the significant effect of state indicates both an effect of location, as Japanese beetles are spreading east to west, and an effect of varying degrees of effort to locate and manage Japanese beetles between the states.

Additionally, time is particularly important for species distribution mapping along an invasion front. Without the temporal variable, the effect of diffusion is lost, which is particularly important in areas where invasive species are expanding their range and there is suitable area which has not yet been utilized (Lodge et al. 2016). Our predictions show that the western spread of Japanese beetles farther into Nebraska and Kansas is more a matter of time than habitat and climate associations. By capturing the expansion of Japanese beetles into new counties over the

5-year period of our study, we were able to model to the near future with current climate and land cover conditions, and without any climate changes, we see that they will likely be present in every county of the region. Our current data and modeling approach enables statistical inference and prediction/forecast at the county level, which is useful for larger scale, regional management of invasive species. Future work for Japanese beetle distribution in this region could focus on abundance data at the point level, which would be more relevant if done in specific land cover types. Such future crop-specific work could be helpful to inform stakeholders of their risk at a more refined level.

Conclusion

In summary, we found that developed areas had a very strong positive relationship with Japanese beetle presence, even at low proportions within the county. Corn and soybean also had a strong positive association with Japanese beetle presence. However, grassland and pasture had an unexpected negative relationship with Japanese beetle presence. This finding underscores the importance of modeling habitat associations at a regional scale, as ecosystems such as grasslands can have regional differences such as species composition, soil morphology, root architecture, and disturbance regimes. This study also provides an example for mitigating bias in community science data by integrating systematic agricultural observations to more accurately evaluate the spread of invasive pests within agroecosystems. Future studies on invasive pests would benefit from accounting for temporal dynamics and enriching citizen science data with agricultural or rural datasets when tracking and predicting invasions. Models incorporating time as a factor at a regional scale, such as ours, can also help identify areas at higher risk of early infestation, enabling more strategic monitoring and resource allocation.

References

- Allsopp, P. G., M. G. Klein, and E. L. McCoy. 1992. Effect of soil moisture and soil texture on oviposition by Japanese beetle and Rose chafer (Coleoptera: Scarabaeidae). *Journal of Economic Entomology* 85:2194–2200.
- Althoff, E. R., and K. B. Rice. 2022. Japanese beetle (Coleoptera: Scarabaeidae) invasion of North America: history, ecology, and management. *Journal of Integrated Pest Management* 13:2.
- Altwegg, R., and J. D. Nichols. 2019. Occupancy models for citizen-science data. *Methods in Ecology and Evolution* 10:8–21.
- Borner, L., D. Martinetti, and S. Poggi. 2022, November 16. A new chapter of the Japanese beetle invasion saga: predicting suitability from long-infested areas to inform surveillance strategies in Europe. *bioRxiv*.
- Borner, L., D. Martinetti, and S. Poggi. 2023. A new chapter of the Japanese beetle invasion saga: predicting suitability from long-invaded areas to inform surveillance strategies in Europe. *Entomologia Generalis*:951–960.
- Borner, L., D. Martinetti, and S. Poggi. 2024. A hitchhiker’s guide to Europe: mapping human-mediated spread of the invasive Japanese beetle. *NeoBiota* 94:1–14.
- Bounoua, L., J. Nigro, P. Zhang, K. Thome, and A. Lachir. 2018. Mapping urbanization in the United States from 2001 to 2011. *Applied Geography* 90:123–133.
- Bowler, D. E., R. J. Boyd, C. T. Callaghan, R. A. Robinson, N. J. B. Isaac, and M. J. O. Pocock. 2024. Treating gaps and biases in biodiversity data as a missing data problem. *Biological Reviews*.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.
- Chen, B. 2020, June 29. CropScapeR: Access Cropland Data Layer Data via the “CropScape” Web Service.
- Climate change 2013: the physical science basis: summary for policymakers, a report of working group I of the IPCC: technical summary. 2013. . Pages 89–91. WMO, UNEP, s.l.
- Davis, A. Y., N. Malas, and E. S. Minor. 2014. Substitutable habitats? The biophysical and anthropogenic drivers of an exotic bird’s distribution. *Biological Invasions* 16:415–427.
- Della Rocca, F., and P. Milanesi. 2022a. The new dominator of the world: Modeling the global distribution of the Japanese beetle under land use and climate change scenarios. *Land* 11:567.
- Della Rocca, F., and P. Milanesi. 2022b. The spread of the Japanese beetle in a european human-dominated landscape: high anthropization favors colonization of *Popillia japonica*. *Diversity* 14:658.
- Dickerson, E. L., and H. B. Weiss. 1918. *Popillia japonica* Newman, a recently introduced Japanese pest. *Canadian Entomology* 50:217–221.
- Dixon, A. P., D. Faber-Langendoen, C. Josse, J. Morrison, and C. J. Loucks. 2014. Distribution mapping of world grassland types. *Journal of Biogeography* 41:2003–2019.
- Edwards, C. R. 1999. Japanese Beetle. Pages 90–91 *Handbook of corn insect pests*. K.L. Steffey, M.E. Rice, J. All, D.A. Andow, M.E. Gray, and J.W. van Duyn (eds.). Entomological Society of America, Lanham, MD.

- Eigenbrode, S., T. Davis, and D. Crowder. 2015. Climate change and biological control in agricultural systems: Principles and examples from North America. Pages 119–135.
- Elahi, E., C. Weijun, H. Zhang, and M. Nazeer. 2019. Agricultural intensification and damages to human health in relation to agrochemicals: Application of artificial intelligence. *Land Use Policy* 83:461–474.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1:330–342.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.
- Fleming, W. E. 1968. Biological Control of the Japanese Beetle. Technical Bulletins.
- Fleming, W. E. 1972. Biology of the Japanese beetle. Technical Bulletin, Agricultural Research Service, USDA.
- Flores, A. 2010. Geraniums Could Help Control Devastating Japanese Beetle : USDA ARS. <https://www.ars.usda.gov/news-events/news/research-news/2010/geraniums-could-help-control-devastating-japanese-beetle/>.
- Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. Third edition. Sage, Thousand Oaks, CA.
- GBIF.org. (n.d.). GBIF Occurrence Download of *Popillia Japonica*. Global Biodiversity Information Facility.
- Gneiting, T., and A. E. Raftery. 2007. Strictly proper scoring rules, prediction, and estimation. *Journal of the American Statistical Association* 102:359–378.
- Grundon, S., and H. Schmucker. 2020. Risk Analysis of Japanese Beetle in Utah. Page 44.
- Hammond, R. B. 1994. Japanese beetle. Pages 64–65 *Handbook of soybean insect pests*. L. G. Higley and D. J. Boethel (eds.). Entomological Society of America, Lanham, MD.
- Hawley, I. M. 1944. Notes on the biology of the Japanese beetle. Page 19. U.S. Department of Agriculture, Bureau of Entomology and Plant Quarterly.
- Hough, A. R., J. R. Nechols, B. P. McCornack, D. C. Margolies, B. K. Sandercock, D. Yan, and L. Murray. 2017. The effect of temperature and host plant resistance on population growth of the soybean aphid biotype 1 (Hemiptera: Aphididae). *Environmental Entomology* 46:58–67.
- Hughes, A. C., J. B. Dorey, S. Bossert, H. Qiao, and M. C. Orr. 2024. Big data, big problems? How to circumvent problems in biodiversity mapping and ensure meaningful results. *Ecography*:e07115.
- Jactel, H., J. Petit, M.-L. Desprez-Loustau, S. Delzon, D. Piou, A. Battisti, and J. Koricheva. 2012. Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology* 18:267–276.
- Khodaverdi, H., T. Fowles, E. Bick, and C. Nansen. 2016. Does drought increase the risk of insects developing behavioral resistance to systemic insecticides? *Journal of Economic Entomology* 109:2027–2031.
- Kistner-Thomas, E. J. 2019. The potential global distribution and voltinism of the Japanese beetle (Coleoptera: Scarabaeidae) under current and future climates. *Journal of Insect Science* 19:16.

Lake, T. A., R. D. Briscoe Runquist, and D. A. Moeller. 2020. Predicting range expansion of invasive species: Pitfalls and best practices for obtaining biologically realistic projections. *Diversity and Distributions* 26:1767–1779.

Lark, T. J., S. A. Spawn, M. Bougie, and H. K. Gibbs. 2020. Cropland expansion in the United States produces marginal yields at high costs to wildlife. *Nature Communications* 11:4295.

Liu, C., C. Wolter, W. Xian, and J. M. Jeschke. 2020. Species distribution models have limited spatial transferability for invasive species. *Ecology Letters* 23:1682–1692.

Lodge, D. M., P. W. Simonin, S. W. Burgiel, R. P. Keller, J. M. Bossenbroek, C. L. Jerde, A. M. Kramer, E. S. Rutherford, M. A. Barnes, M. E. Wittmann, W. L. Chadderton, J. L. Apriesnig, D. Beletsky, R. M. Cooke, J. M. Drake, S. P. Egan, D. C. Finnoff, C. A. Gantz, E. K. Grey, M. H. Hoff, J. G. Howeth, R. A. Jensen, E. R. Larson, N. E. Mandrak, D. M. Mason, F. A. Martinez, T. J. Newcomb, J. D. Rothlisberger, A. J. Tucker, T. W. Warziniack, and H. Zhang. 2016. Risk analysis and bioeconomics of invasive species to inform policy and management. *Annual Review of Environment and Resources* 41:453–488.

Menke, S. B., D. A. Holway, R. N. Fisher, and W. Jetz. 2009. Characterizing and predicting species distributions across environments and scales: Argentine ant occurrences in the eye of the beholder. *Global Ecology and Biogeography* 18:50–63.

Morefield, P. E., S. D. LeDuc, C. M. Clark, and R. Iovanna. 2016. Grasslands, wetlands, and agriculture: the fate of land expiring from the Conservation Reserve Program in the Midwestern United States. *Environmental Research Letters* 11:094005.

Nebraska Department of Agriculture. (n.d.). Survey and Detection Program. <https://nda.nebraska.gov/>.

Niziolek, O. K., M. R. Berenbaum, and E. H. DeLucia. 2013. Impact of elevated CO₂ and increased temperature on Japanese beetle herbivory. *Insect Science* 20:513–523.

NOAA National Centers for Environmental Information. 2023, March. Climate at a Glance: County Time Series. NOAA National Centers for Environmental information.

Paini, D. R., A. W. Sheppard, D. C. Cook, P. J. De Barro, S. P. Worner, and M. B. Thomas. 2016. Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences* 113:7575–7579.

Petty, B. M., D. T. Johnson, and D. C. Steinkraus. 2015. Changes in abundance of larvae and adults of *Popillia japonica* (Coleoptera: Scarabaeidae: Rutelinae) and other white grub species in Northwest Arkansas and their relation to regional temperatures. *Florida Entomologist* 98:1006–1008.

Potter, D. A., and D. W. Held. 2002. Biology and management of the Japanese beetle. *Annual Review of Entomology* 47:175–205.

Potter, D. A., A. J. Powell, P. G. Spicer, and D. W. Williams. 1996. Cultural Practices Affect Root-Feeding White Grubs (Coleoptera: Scarabaeidae) in Turfgrass. *Journal of Economic Entomology* 89:156–164.

Prakash, A., J. Rao, A. K. Mukherjee, J. Berliner, S. S. Pokhare, T. Adak, S. Munda, P. R. Shashank, Applied Zoologists Research Association, and Central Rice Research Institute (India). 2014. Climate change: impact on crop pests. Applied Zoologists Research Association (AZRA), Central Rice Research Institute, Cuttack, Odisha, India.

R Core Team. 2022. R version 4.2.1 (2022-06-23) -- "Funny-Looking Kid".

Roy, H. E., A. Pauchard, P. Stoett, T. Renard Truong, S. Bacher, B. S. Galil, P. E. Hulme, T. Ikeda, K. Sankaran, M. A. McGeoch, L. A. Meyerson, M. A. Nuñez, A. Ordóñez, S. J.

- Rahlao, E. Schwindt, H. Seebens, A. W. Sheppard, and V. Vandvik. 2024. IPBES Invasive Alien Species Assessment: Summary for Policymakers. Zenodo.
- Shanovich, H. N., A. N. Dean, R. L. Koch, and E. W. Hodgson. 2019. Biology and management of Japanese beetle (Coleoptera: Scarabaeidae) in corn and soybean. *Journal of Integrated Pest Management* 10:9.
- Skendžić, S., M. Zovko, I. P. Živković, V. Lešić, and D. Lemić. 2021. The impact of climate change on agricultural insect pests. *Insects* 12:440.
- Smith, L. B., and C. H. Hadley. 1926. The Japanese beetle. Washington, D.C. : U.S. Dept. of Agriculture.
- Thomson, L. J., S. Macfadyen, and A. A. Hoffmann. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control* 52:296–306.
- Thurman, J. H., D. W. Crowder, and T. D. Northfield. 2017. Biological control agents in the Anthropocene: current risks and future options. *Current Opinion in Insect Science* 23:59–64.
- Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences* 108:20260–20264.
- Urbaneja-Bernat, P., V. Ibáñez-Gual, M. Montserrat, E. Aguilar-Fenollosa, and J. A. Jaques. 2019. Can interactions among predators alter the natural regulation of an herbivore in a climate change scenario? The case of *Tetranychus urticae* and its predators in citrus. *Journal of Pest Science* 92:1149–1164.
- USDA National Agricultural Statistics Service. 2022. Cropland Data Layer. Published crop-specific data layer [Online]., USDA NASS Marketing and Information Services Office, Washington, DC.
- Walker, K. 2016. tigris: An R Package to Access and Work with Geographic Data from the US Census Bureau. *The R Journal* 8:231–242.
- Walker, K. 2024. tigris: Load Census TIGER/Line Shapefiles.
- Weaver, J. E., and T. J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of Tall-Grass Prairie. *Botanical Gazette* 93:113–150.
- Wiersma, Y. F., F. Huettmann, and C. A. Drew. 2011. Introduction. Landscape Modeling of Species and Their Habitats: History, Uncertainty, and Complexity. Pages 1–6 in C. A. Drew, Y. F. Wiersma, and F. Huettmann, editors. *Predictive Species and Habitat Modeling in Landscape Ecology: Concepts and Applications*. Springer, New York, NY.
- Wood, S. N. 2011. Fast Stable Restricted Maximum Likelihood and Marginal Likelihood Estimation of Semiparametric Generalized Linear Models. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 73:3–36.
- Wood, S. N. 2017. *Generalized Additive Models: An introduction with R*. Second edition. Chapman and Hall/CRC.
- Woodcock, B. A., N. J. B. Isaac, J. M. Bullock, D. B. Roy, D. G. Garthwaite, A. Crowe, and R. F. Pywell. 2016. Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications* 7:12459.
- Zhang, X., T. J. Lark, C. M. Clark, Y. Yuan, and S. D. LeDuc. 2021. Grassland-to-cropland conversion increased soil, nutrient, and carbon losses in the US Midwest between 2008 and 2016. *Environmental Research Letters* 16:054018.
- Zhu, G., H. Li, and L. Zhao. 2017. Incorporating anthropogenic variables into ecological niche modeling to predict areas of invasion of *Popillia japonica*. *Journal of Pest Science* 90:151–160.

**Chapter 4 - Investigating a semiochemical-based mechanism for the
beneficial activity of sorghum intercropped with soybeans on
management of *Popillia japonica***

Submitted as: Kuchеров N.B., Hetherington M.C., Gerken A.R., Morrison W.R., and Kim T.N.

Investigating a semiochemical-based mechanism for the beneficial activity of sorghum
intercropped with soybeans on management of *Popillia japonica*.

Abstract

Japanese beetle, *Popillia japonica* Newman, is an invasive species that attacks many field and ornamental crops. Intercropping soybean with sorghum is suggested as a strategy to reduce the abundance of *P. japonica* within and movement *P. japonica* throughout soybean fields. The mechanism by which this affects *P. japonica* is unknown, but may arise from olfactory cues emitted by the intercrop as *P. japonica* responds to host plant compounds. In this study, we investigated a semiochemical-based mechanism for the behavioral response of *P. japonica* to intercropping soybean with sorghum by 1) evaluating *P. japonica* behavioral responses to solvent extracts from monocropped soy, intercropped soy, and a mixture of soy and sorghum extracts in no-choice video-tracking and preference in a release-recapture dual-choice assay to host stimuli from plants; and 2) applying solid-phase microextraction (SPME) in conjunction with gas chromatography coupled with mass spectrometry (GC-MS) to characterize the semiochemical profiles of each extract. We found unique semiochemical profiles among our treatments, with 1-octen-3-ol and 1-octanol characteristic of monocropped soybean and dodecane-1-iodo primarily in sorghum extracts. Nevertheless, our treatments did not significantly affect movement or orientation by individual *P. japonica* compared to controls, nor did conspecifics exhibit a significant preference for any of the treatments in a dual-choice assay at a local scale. Therefore, if intercropping soybean with sorghum significantly effects the behavior of *P. japonica* in the field, it must occur at a different scale, or in response to non-olfactory stimuli (e.g., visual, habitat, or landscape cues) rather than semiochemical cues.

Introduction

Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), is an economically important invasive pest of over 300 plants, including soybean (Shanovich et al. 2019). The species arrived in the USA in 1916 and various quarantine programs have been in place to control their spread, including the U.S. Domestic Japanese Beetle Domestic Harmonization Plan (National Plant Board 1998). *Popillia japonica* are moving westward across the USA and their spread throughout the Great Plains is predicted to advance in the coming years (Kucherov et al. 2025), which is particularly concerning due to the threat they pose to key U.S. crops such as soybean and corn (Shanovich et al. 2019). Although soybean can withstand high amounts of *P. japonica* defoliation before yield loss (Todd and Morgan 1972), studies have shown that the amount of damage varies with growth period, with high amounts of defoliation after bloom or during pod set affecting yield substantially more than during vegetative growth (Gould 1963). Currently, the main way to manage *P. japonica* infestation is to spray pesticides such as pyrethroids and neonicotinoids, but this is not an effective strategy because fields are quickly reinfested by new immigrating populations of *P. japonica* as they are strong flyers and disperse long distances (Potter et al. 2006, Shanovich et al. 2019). A recent study on *P. japonica* flight distances found that the majority of marked individuals (75%) moved 5–9 km, with one individual traveling 12 km in 24 h (Lessio et al. 2021). Therefore, other management strategies are needed to effectively control this insect pest.

Behavioral control using semiochemicals may be an effective management strategy. *Popillia japonica* are known to respond to a variety of olfactory cues, including their sex pheromone, (R,Z)-5-(–)-(dec-1-enyl)oxacyclopentan-2-one (Tumlinson et al. 1977), through highly sensitive neurons in their antennae (Ishida and Leal 2008, Wang et al. 2026). A

combination of semiochemicals from plant volatile organic compounds (VOCs) and the female-produced sex pheromone create a highly effective lure (Klein et al. 1981), these lures are commercially available and are commonly used to attract-and-kill *P. japonica* in home gardens and small farms. *Popilla japonica* also relies on olfactory cues for locating host plants and determining host preferences (Ahmad 1982). Previous studies found that *P. japonica* are attracted to various undamaged plant volatiles and herbivore-induced volatiles (Loughrin et al. 1995, 1998). Differences in the volatile profiles of susceptible and non-susceptible cultivars have been shown to affect *P. japonica* preference in maples (Loughrin et al. 1996, 1997) and grapes (Gu and Pomper 2008). Therefore, it is possible that changes to a host plant's semiochemical profile could affect host selection and preference by *P. japonica*.

In particular, the behavioral response by herbivores to host plant semiochemicals can be disrupted by changes to patch-level semiochemical emissions when multiple plant species are together in a patch (Visser and Avé 1978, Späthe et al. 2013) or through emission of particularly repellent compounds (Wei et al. 2025). Plants commonly use volatile organic compounds (VOCs) and secondary metabolites to “call” in mutualistic predators and parasitoids of herbivores, attract pollinators, or repel antagonists (Dicke 2009), and as a means of communication between neighboring plants (Baldwin 2010, Ninkovic et al. 2021). Volatile profiles are generally species-specific and dynamic over time (Blaauw et al. 2019), and the chemical classes within the bouquet of volatiles emitted from plants can be used to identify species (Vivaldo et al. 2017). However, volatile emissions can also change based on the identity of neighboring plants (Kigathi et al. 2019) and intercropping has been shown to help prevent immigration of pests into the cash crop in other systems (Blaauw et al. 2019) and/or to disrupt the olfactory perception of insect pests (Peter et al. 2023, Fyie et al. 2025). Thus, location of a

host plant through olfactory cues by the herbivore could be disrupted because of changes to the host plant's own semiochemical profile in the presence of the intercropped species or through the mixing of volatiles by the intercropped species with the host plant, changing the VOC fingerprint at the patch-level. These patterns are supported by the resource concentration hypothesis, which states that specialist herbivores are better able to locate and persist in patches with higher or purer densities of their host plants (Root 1973). Indeed, intercropping has been shown to reduce pest populations and reduce yield loss (Trenbath 1993, Ampong-Nyarko et al. 1994, Duru et al. 2015, Guinet et al. 2023, Akchaya et al. 2025) in some cropping systems.

Historically, it was thought that the pattern of intercropping could disrupt *P. japonica* movement through fields and reduce their population abundance. However, not all types of intercropping resulted in a reduction of *P. japonica* infestations. For example, intercropping soybeans with maize resulted in higher abundances of *P. japonica* than in monocropped soybean (Tonhasca 1994) and beetle abundance in soybean also increased when rye was used as a cover crop (Smith et al. 1988). One alternative integrated pest management (IPM) strategy suggested for *P. japonica* in soybean is intercropping with sorghum, which claims to disrupt movement and reduce beetle abundances. This recommendation was based on previous studies that evaluated the movement of *P. japonica* through intercropped fields of soybean and sorghum (Bohlen and Barrett 1990, Holmes and Barrett 1997). The mechanism by which the combination of sorghum and soybean affects *P. japonica* behavior remains unknown, and it may result from visual or chemical cues. Holmes and Barrett (1997) concluded that the intercropped sorghum with soybean in their experiment “inhibit Japanese beetle movement apparently by conferring ‘associational resistance’ in the cropping system” and indicated that they believed that this behavior was mediated through semiochemicals and/or secondary metabolites.

As a result, this study aimed to evaluate a semiochemical-based mechanism for the *P. japonica* pattern of abundance found in Bohlen and Barrett (1990) and Holmes and Barrett (1997). To this end, we (i) characterized the semiochemicals from intercropped soy and compared the chemical profile to monocropped soy and a mixture of soy and sorghum, (ii) evaluated the effect of these semiochemicals on the movement by *P. japonica*, and (iii) evaluated their preference in a dual-choice release-recapture assay. We hypothesized that the semiochemical profile of the intercropped soybean would be significantly different from that of monoculture soybeans. In addition, based on prior work, we hypothesized that *P. japonica* will favor the monocropped soybeans over intercropped soybeans, and that beetles will be attracted to the monocropped soybean significantly more than the intercropped soybean or a mixture of monocropped soybean and sorghum in the release-recapture assay.

Insights from this study could lead to improved management strategies because if intercropping with non-preferred crops, (e.g., sorghum) reduces the abundance of *P. japonica* in soybean fields by interfering with their ability to locate the field as a suitable host, then its use could reduce the amount of pesticide and energy inputs used to manage these pests. Additionally, identifying the mechanism for this behavioral effect as arising from either changes in VOCs due to plant identity or olfactory confusion from patch-level differences may provide us with a way to test future intercropping combinations for effectiveness in other crops. Attract-and-kill traps are widely used for *P. japonica*, but one of the limitations is that they attract additional individuals from kilometers away. Novel stimuli that can be used to target *P. japonica* in localized management efforts and an improved knowledge of this aspect of *P. japonica* behavior could lead to improvements in lure formulation and behavioral control.

Methods

Study system

This study was conducted in NE Kansas at KSU and at USDA..... Soybean (var. Pioneer P42A84E) and sorghum (var. Pioneer 85P58) were planted in plots at Kansas State University's North Farm fields (location = 39.206550, -96.593667) on May 13, 2025. Row spacing was 30" (=76.2 cm) for both species. We used soybeans plants from within the same field to control for environmental effects on semiochemical profiles, as evidence shows that differences in soil profiles or agricultural management choices such as crop rotation can alter the semiochemical profiles of plants (Malone et al. 2020, Interian-Aguíñaga et al. 2025). Intercropped soybean extracts were taken from the row of soybean directly touching sorghum because communication between neighboring plants, both above and below ground, occurs at short distances, typically less than 1 meter (Heil and Karban 2010, Heil and Adame-Álvarez 2010, Gao et al. 2014). Monocropped soybean extracts were taken from soybean plants surrounded by soybean for at least 5 rows on each side. The soy-sorghum-mixture was a combination of monocropped soybean extract and sorghum extract. This configuration allows us to test separately the hypotheses that *P. japonica* behavior is affected by (1) changes to the host plant's own semiochemical profile (intercropped soybean) or (2) the mixing of volatiles by the intercropped species (sorghum) with the host plant (soybean).

Popillia japonica were collected daily from wild populations in Riley and Pottawatomie Co. during Jul–Aug 2025, with no-kill Japanese/Oriental beetle pheromone traps (Rescue International, Spokane, WA, USA). Traps were hung near home gardens, to avoid capturing beetles from agricultural fields. Beetles were kept in 25 × 25 cm plastic tubs with a bedding of moistened peat and River birch (*Betula nigra*) leaves and Virginia creeper (*Parthenocissus*

quinquefolia) vines as food. Food was maintained ad libitum prior to use in the experiments below.

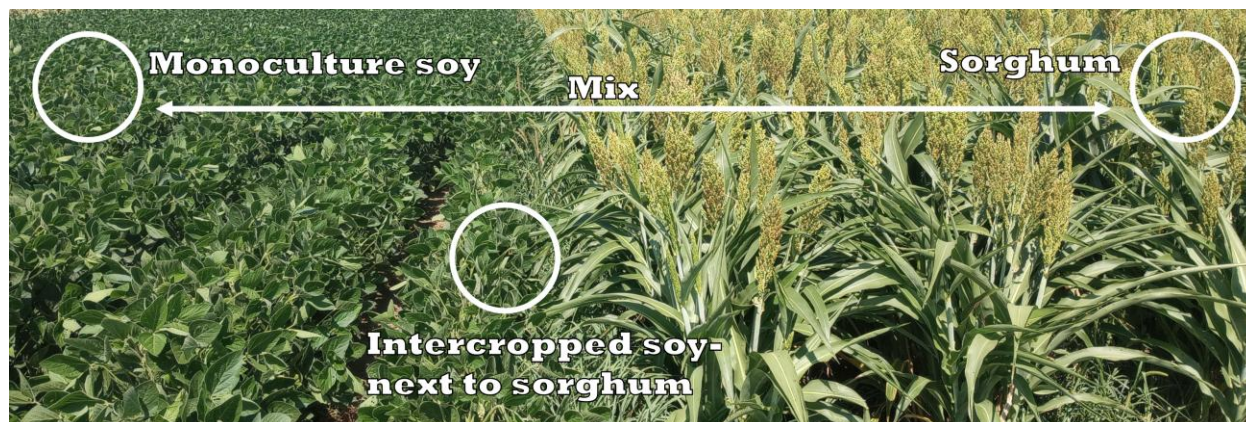


Figure 4-1 Layout of the field plot; intercropped soybean plants were planted directly next to sorghum, while monocropped soybean plants were surrounded by soybean.

Plant Semiochemical Extracts

We characterized the chemical profile of plants using extracts taken from fresh samples, in the field on 5 August 2025. Intercropped soybean samples were taken from soybean planted directly next to sorghum, while monocropped soybean samples were taken from soybean plants in the middle of the field (Figure 1). Media storage jars (250-mL capacity) were cleaned with methanol, hexane, and dichloromethane. Afterwards, 100 ml of dichloromethane was added to each jar (MilliporeSigma, Burlington, MA, USA), and the jars were brought to the field on ice. For each soybean plant, 3 top leaves and 2 new trifolds were removed and placed into dichloromethane. For each sorghum plant, 1 apicol, approximately 50% of the leaf, and 5 racemes were removed and placed into 100 mL of dichloromethane. Samples were vigorously shaken for 30 seconds, then placed on ice for 1 h before filtration. Extracts were decanted through filter paper 85 mm (Grade 1, Whatman, Global Life Sciences Solutions, Buckinghamshire, UK) into fresh, clean mason jars and then stored at -20°C until use. Leaves

were left overnight to evaporate DCM. Leaves were placed in the oven in the morning to dry, and a dry weight was taken with a balance (Sartorius AG, Göttingen, Germany).

Chemical analysis with GC-MS

Solid-phase microextraction (SPME) employing a DVB/Carboxen/PDMS fiber (57329-U, Supelco, MilliporeSigma, St. Louis, MO, USA) was conducted to quantify the volatiles present in each solvent extract. A total of 50 μL aliquots of each sample were applied to a 1-cm diameter filter paper disc (Ahlstrom-Munksjö, Mt. Holly Springs, PA, USA) along with 2 μL of tetradecane as an internal standard and allowed to dry. Discs were then transferred into 20 ml headspace vials (093640-036-00, Gerstel Inc., Linthicum Heights, MD, USA) and sealed with a magnetic screw cap with a PTFE-backed septum (093640-040-00, Gerstel Inc.). Headspace vials were incubated at 60°C for 15 min without agitation to facilitate movement of compounds into the vial headspace before the SPME fiber was exposed to the headspace above the sample for 60 min. Samples were analyzed on an Agilent 7890B gas chromatograph (GC) equipped with an Agilent Durabond HP-5 column (30 m length, 0.250 mm diameter, 0.25 μm film thickness) and He as the carrier gas at a constant 1.2 mL min^{-1} flow rate and 40 cm s^{-1} velocity, which was coupled with a single-quadrupole Agilent 5977B mass spectrometer (MS). SPME fibers were desorbed in the inlet operated in splitless mode of the GC at 250°C for 3 min. The oven was initially maintained at 35°C for 3 min before increasing to 180°C at a rate of 10°C min^{-1} . The oven temperature then increased from 180–250°C at 20°C min^{-1} , where it was held for 2 min. Mass spectra were scanned from 35 to 550 m/z for the entire length of the run. A mixture containing C8–C20 alkanes was employed to calculate Kovats index for all peaks. Compounds were preliminarily identified by comparison of spectral data with those from the NIST 14 library

and by GC retention index and Kovats index (Adams 2007). The identities of 1-octen-3-ol and Octanol were subsequently confirmed by comparing their retention times and mass spectra to authentic commercial standards from MilliporeSigma.

Video-tracking Assay with Ethovision

Video-tracking coupled with Ethovision software v.14.0 (Noldus, Inc., Leesburg, VA, USA) was used to analyze *P. japonica* responses to the plant extracts. Six arenas consisting of Petri dishes (100 × 20 mm; VWR International, Radnor, PA, USA) with an 85-mm filter paper (Grade 1, Whatman; GE Healthcare, Chicago, IL, USA) adhered to the bottom using double-sided sticky tape were arranged below a network video camera (GigE, Basler AG, Ahrensburg, Germany). The entire setup was situated in a walk-in environmental chamber (Percival Scientific, Perry, IA, USA) set to constant 27.5°C, and 60% relative humidity during the photophase when beetles are most active. Treatment extracts consisted of (1) 50 µL of monoculture soy extract, (2) 50 µL of intercropped soy (soy grown alongside sorghum) extract, and (3) a mixture of 50 µL of monoculture soy and 50 µL sorghum extract placed on a 1-cm diameter filter paper and allowed to evaporate prior to use. The control consisted of 50 µL of neat dichloromethane on a 1-cm diameter filter paper and allowed to evaporate for the same period. A filter paper with a given treatment was placed on one side of the arena, and a filter paper of neat solvent (DCM) was placed on the opposite side of the arena (Figure 2a). Treatment sides were alternated, and the position of treatments was systematically rotated to avoid positional bias.

Within each Petri dish, four zones were monitored, including the two halves of the Petri dish arena (i.e. treatment half versus control half) and the two 1 cm diameter stimulus zones

nested in the center of each half where stimuli were applied (treatment stimulus zone and control stimulus zone). *Popillia japonica* were starved separately for 1 h prior to testing. The movement of individual beetles within each arena was simultaneously recorded on an adjacent computer, and after the experiment was finished, loaded into Ethovision with the appropriate detection and arena settings. We used Ethovision to record the distance moved and instantaneous velocity, as well as frequency entering, duration spent in, and latency to finding each half of the arena and the stimulus zones. For each assay, a single beetle was placed at the bottom center of an arena and allowed to interact with the extract and control with movement recorded over 10 min. A time of 10 min was used after testing testing multiple time periods, and finding that individuals stopped making decisions after 10 min. Within a small arena such as a petri dish, the area becomes saturated after a longer time. A total of $n = 24$ replicate adults were tested per treatment.

Preference Assay

To incorporate group dynamics and *Popillia japonica* response to fresh plant cuttings, we performed a release-recapture assay in large plastic containers ($25 \times 25 \times 26$ cm) with moistened peat placed in large walk-in environmental chambers (Percival Scientific). Beetle locations were recorded after 1 h to infer initial choice and after 24 h to infer final choice after other beetles had begun feeding or if beetles reject the initial choice after finding the plant unpalatable. Chambers were set to constant 28°C and 65% relative humidity with 16:8 L:D to mimic summer conditions. Soybean leaf cuttings consisted of one trifoliate and its petiole, while sorghum cuttings consisted of one raceme and two leaf portions weighing approximately 100 g each. Cuttings were placed directly on ice from the field and remained on ice for 1 h before the trial began. Plant petioles were placed into water in vaccine vials (Becton Dickinson, Franklin Lakes, NJ,

USA) and closed with parafilm to maintain freshness then inserted into the peat flush at ground level to stand up at opposite sides of the chamber. Large plastic containers were divided into 5 equally-sized (5 cm) zones with a treatment on opposite sides of each container. Specifically, the central release zone was zone 3, while zone 1 and zone 5 contained stimuli (Figure 2b). The treatment combinations were as follows; (i) monoculture soy versus intercropped soy (intersoy; soy next to sorghum); (ii) monoculture soy versus a mix of mono soy and sorghum; (iii) monoculture soy versus sorghum; (iv) intercropped soy versus a mix of mono soy and sorghum. Soybean trifolds were paired with similarly-sized trifolds within each container. A total of four unsexed beetles were placed at the center of each container. After 1 h and 24 h, beetle locations were recorded by zone. Beetles who had reached the stimulus zones (zones 1, 5) or moved toward the stimulus zone (zones 2, 4) were counted for the corresponding option. Beetles that did not leave the central zone (zone 3) after the response time were recorded as non-responsive and included in the final analysis as no choice.

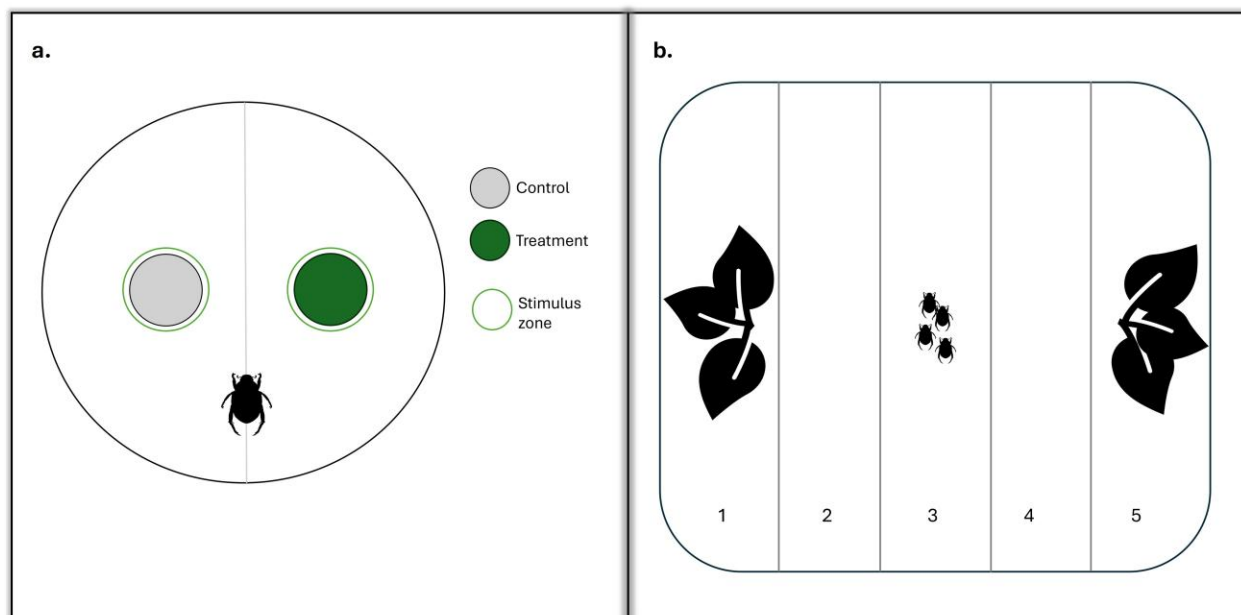


Figure 4-2 Video tracking assays with Ethovision (a) were conducted in a petri dish with a treatment extract on one side and a control extract on the other side. Each stimulus had a defined stimulus zone and a treatment side. Groups of *P. japonica* were released in dual choice assays (b) and recaptured after 1 h and 24 h. Dual choice assays had 5 zones, with treatments of fresh plant cuttings in zones 1 and 5.

Statistical analysis

Volatile profiling

Data were compiled using Masshunter Unknowns Analysis (Agilent Inc.) and compounds were aligned with the R package uafR (Stratton et al. 2024). Siloxane and phthalate peaks were removed as these represent common contaminants in GC-MS analysis. All other volatiles exceeding 80% similarity to the reference library and occurring in more than one sample were retained in the analysis. Standardized abundance of each compound was converted to ng per g of dry biomass weight based on the compound peak area relative to the tetradecane internal standard. The PermDisp2 procedure was employed to assess homogeneity of group dispersions (Anderson et al. 2006), and a permutational multivariate analysis of variance (PERMANOVA) was applied to compare extract composition across treatments. Following a significant global

test, PERMANOVA was applied in a pairwise manner to determine which treatments could be differentiated based on volatile emissions. The Holm-Bonferroni method was employed to control family-wise error rate during multiple comparisons testing. Pairwise Bray-Curtis similarities were calculated between samples and non-metric multidimensional scaling (NMDS) was applied to visualize differences in extract composition among treatments. A total of $n = 1000$ permutations were used for the ordination procedure and a stress value < 0.05 indicated that an excellent representation of the original dataset in the $k = 2$ dimensions. Similarity percentage (SIMPER) analysis was applied to assess the relative importance of variables to differences between treatments using the package *vegan* in R (Oksanen et al. 2025). For all analyses, R Software was used (R Core Team 2025), and unless otherwise specified, $\alpha = 0.05$. Finally, indicator analysis using the *indicspecies* package was employed to identify constituents that strongly contributed to differences among treatment groups (Cáceres and Legendre 2009) and calculate the indicator values (Dufrêne and Legendre 1997).

Video-tracking Assay with Ethovision

To analyze behavior in the video-tracking assay, we first calculated the proportional differences between treatment and control zones. Preference indices (PIs) for distance, velocity, and frequency were calculated for both the stimulus zones and each half of the arena as $(\text{treatment value} - \text{control value}) / (\text{treatment value} + \text{control value})$, while cumulative duration and latency responses were calculated as $(\text{treatment value} - \text{control value}) / (600 \text{ seconds})$. This index could vary from -1 to 1, with full preference at 1, no difference at 0, and full repellency at -1. For each treatment group (monoculture soy, soy-intercropped, soy-sorghum-mix), one-sample t-tests were used to test whether the mean preference index differed from zero. Differences across

treatments were visualized as differences between treatment and control values (treatment–control), with log values used for latency, using ggplot2 in R (Wickham 2016).

Behavioral comparisons across treatments were analyzed using generalized linear mixed models with the glmmTMB package (McGillucuddy et al. 2025). Movement data was modeled using the appropriate distribution for each variable, with treatment zone (half of the Petri dish) and kernel zone (1 cm stimulus area) analyzed separately. Distance and velocity were analyzed with Tweedie models to account for the non-negative, right skewed structure which included zeros. Count variables such as frequency within zones and movement frequency were modeled with Negative binomial or zero-inflated Negative binomial distributions. Continuous variables such as cumulative duration, latency, and time mobile were modeled using Gamma or zero-inflated Gamma distributions. Residuals were checked through visual inspection and formal testing of overdispersion and zero-inflation using the DHARMA package (Hartig 2025). Models for movement variables with multiple zones per dish included interactions between treatment and zone and dish as a random variable. Post-hoc comparisons with Tukey’s HSD were performed using the package emmeans to get pairwise comparisons across treatments.

Preference Assay

For the release-recapture preference assay, the probability of beetles choosing each option (option 1, option 2, or no choice) was compared through generalized linear models fit using base R functions or multinomial logistic mixed models fit using the glmer function from the package lme4 (Bates et al. 2015), with individual beetle choices recorded, treatment as a main effect and trial number as a random effect. If trial number did not improve fit (determined through anova() comparison between the mixed model and the generalized linear model containing only treatment as a main effect), then the model without the mixed effect was used.

Average predicted values for each choice were calculated on the response scale using the emmeans package (Lenth and Piaskowski 2025), and pairwise comparisons were made across the choices, using Tukey's HSD (Honestly Significant Difference) to adjust for multiple comparisons.

Results

Plant Semiochemical Profiles

Semiochemical profiles were significantly different across treatments (PERMANOVA, $R^2 = 0.69$, $p = 0.001$, Figure 3), and these differences were not due to heterogeneity in dispersion (PERMDISP, $P > 0.5$). We found that 1-octen-3-ol, nonanoic acid, 1H-indene-2,3-dihydro (hereafter referred to as indane) together explained 77.1% of the differences between monoculture soy (mono-soy) and intercropped soy (inter-soy) (i.e., simpler analysis, Table 1). 1-octen-3-ol (Figure 4a) and nonanoic acid (Figure 4b) were found in higher abundances in mono-soy than inter-soy, while indane (Figure 4c) was present in mono-soy but not inter-soy. Dissimilarity between mono-soy and the mixture of sorghum and soy (mix) were explained by 1-octen-3-ol, indane, and nonanoic acid (73.3%), while the majority of dissimilarity between inter-soy and mix was explained by 1-octen-3-ol, (2,4)-Di-tert-butylphenol (Figure 4d), and nonanoic acid (78.5%). Three indicator species were associated with two groups. The compounds 1-octen-3-ol (Indicator Value [IndVal] = 0.936, $P = 0.01$, Figure 4a) and 1-octanol (IndVal= 0.936, $p = 0.01$, Figure 4e) were associated with the group of mono-soy and mix, while Dodecane-1-iodo (IndVal= 0.912, $p < 0.05$, Figure 4f) was associated with sorghum and mix. Overall, there were 7.7–51-fold higher abundance of compounds in extracts from mono-soy, inter-soy, and mix

treatments compared to sorghum alone (Table 2). All the treatments had similar alpha chemical diversity with 20–26 compounds.

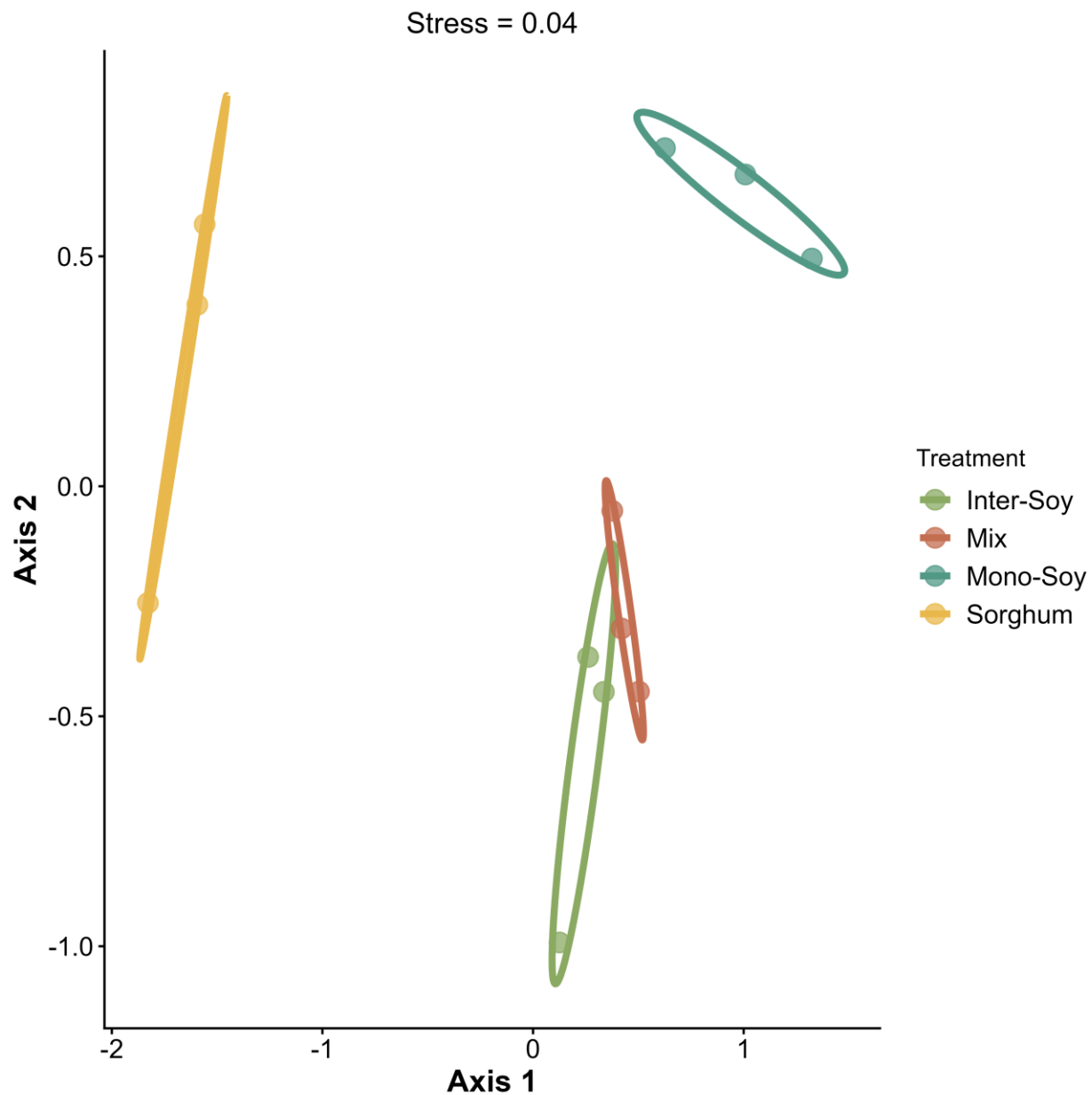


Figure 4-3 Non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis similarities among plant semiochemical extracts from intercropped soybean (inter-soy), monocropped soybean (mono-soy), soybean-sorghum mix (mix), and sorghum. Points represent individual samples, colored by treatment. Ellipses indicate 95% confidence intervals around group centroids. The stress value was 0.04.

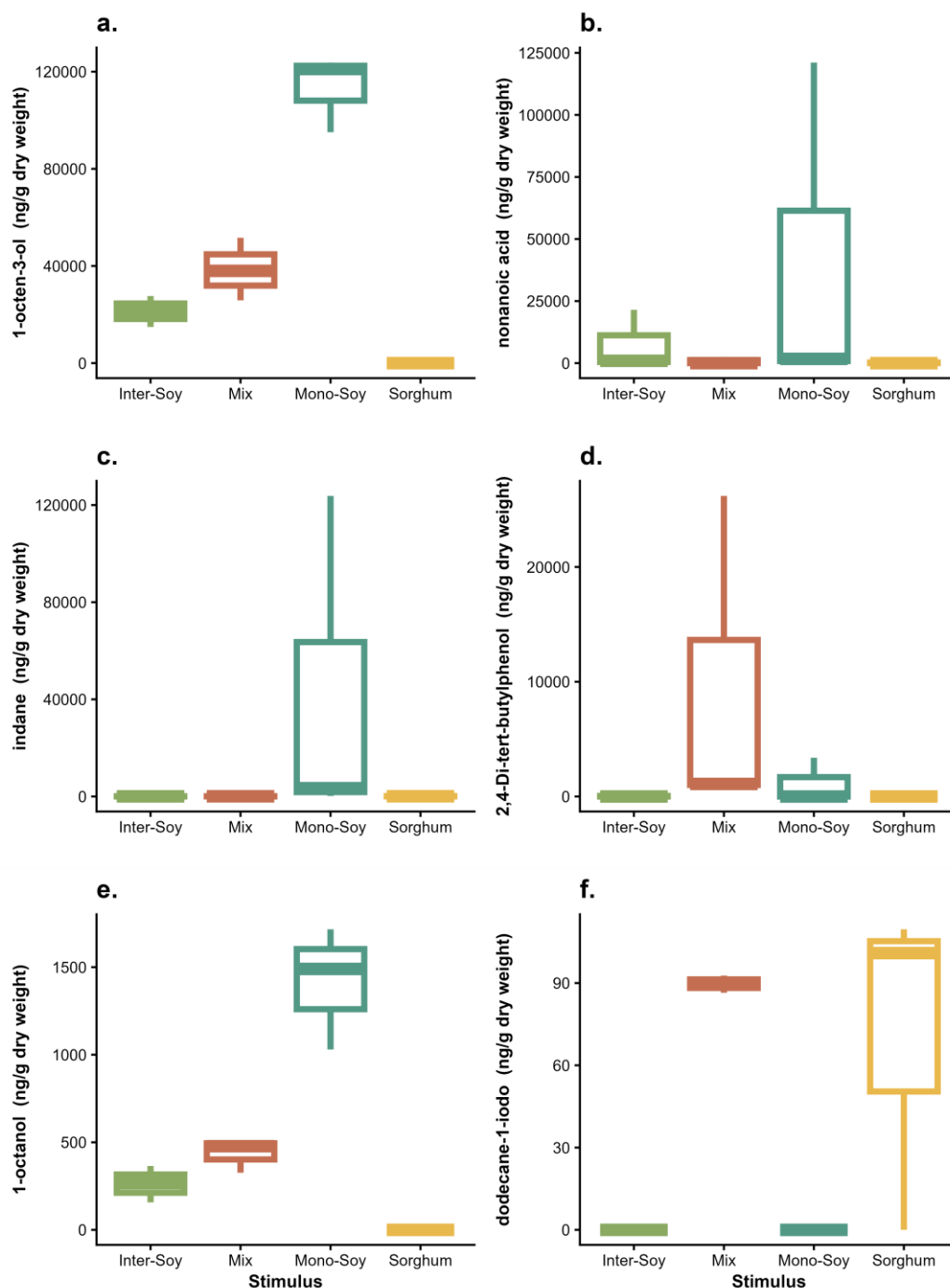


Figure 4-4 Six compounds from the plant semiochemical extracts were associated with significant differences between treatments, including 1-octen-3-ol (a), nonanoic acid (b), indane (c), 2,4-Di-tert-butylphenol (d), 1-octanol (e), and Dodecane-1-iodo (f). Abundances of each compound across all samples by treatments are shown as boxplots in ng g⁻¹ with thick horizontal lines representing medians, boxes representing the interquartile ranges, and whiskers representing the ranges. Abbreviations: mono soy = monocropped soy, inter soy = intercropped soy, mix= soy-sorghum-mix.

Table 4-1 Simper results identifying compounds responsible for the differences between treatments

COMPOUND	AVERAGE	SD	RATIO	CUMULATIVE SUM	P
Monoculture Soy v. Intercropped Soy					
1.Octen.3.ol	0.33	0.028	12	0.41	0.58
Nonanoic.acid	0.15	0.19	0.80	0.59	0.30
Indane	0.14	0.21	0.70	0.77	0.13
2.Oxo.4.phenyl.6..4.chlorophenyl..1.2.dihydropyrimidine	0.13	0.20	0.67	0.94	0.20
Dodecane..4.6.dimethyl.	0.020	0.026	0.77	0.96	0.50
Monoculture Soy v. Soy-Sorghum-Mix					
1.Octen.3.ol	0.26	0.048	5.3	0.36	0.92
Indane	0.14	0.20	0.70	0.55	0.25
Nonanoic.acid	0.13	0.19	0.68	0.73	0.39
2.Oxo.4.phenyl.6..4.chlorophenyl..1.2.dihydropyrimidine	0.12	0.19	0.67	0.91	0.29
2.4.Di.tert.butylphenol	0.032	0.042	0.78	0.95	0.48
Monoculture Soy v. Sorghum					
1.Octen.3.ol	0.47	0.0038	120	0.47	0.057
Indane	0.16	0.23	0.70	0.64	0.0010
Nonanoic.acid	0.16	0.23	0.68	0.80	0.23
2.Oxo.4.phenyl.6..4.chlorophenyl..1.2.dihydropyrimidine	0.16	0.23	0.67	0.95	0.0070
2.Propanone..1.methoxy.	0.0090	0.013	0.70	0.96	0.16
Intercropped Soy v. Soy-Sorghum-Mix					
1.Octen.3.ol	0.20	0.12	1.6	0.41	0.98
2.4.Di.tert.butylphenol	0.10	0.14	0.74	0.62	0.17
Nonanoic.acid	0.078	0.10	0.76	0.78	0.71
Dodecane..4.6.dimethyl.	0.062	0.090	0.69	0.91	0.36
Undecane..4.7.dimethyl.	0.0063	0.0066	0.95	0.93	0.39
Intercropped Soy v. Sorghum					
1.Octen.3.ol	0.54	0.17	3.1	0.57	0.022
Nonanoic.acid	0.15	0.21	0.73	0.74	0.27
Dodecane..4.6.dimethyl.	0.14	0.21	0.69	0.89	0.0030
3.Buten.2.ol..2.methyl.	0.019	0.016	1.2	0.91	0.18
Glycidol	0.013	0.0079	1.6	0.92	0.12

Table 4-2 Compounds identified by SPME-GC/MS from extracts of monoculture soybean, intercropped soybean, mized soybean and sorghum, and sorghum alone. Means $\pm$ SE represent compounds in ng g⁻¹ dry biomass (shaded from low values in browns to high values in blue-greens)

COMPOUND ^{1,2}	RT (MIN)	Mono-Soy			Inter-Soy			Mix			Sorghum		
		MEAN ^{3,4}	SE	% OF TOTAL	MEAN ^{3,4}	SE	% OF TOTAL	MEAN ^{3,4}	SE	% OF TOTAL	MEAN ^{3,4}	SE	% OF TOTAL
X2.Propanone..1.methoxy.	2.023018	2,000	2,000	0.980	0	0	0	0	0	0	100	100	2.29
X3.Buten.2.ol.2.methyl.	3.163101	300	300	0.126	100	80	0.323	400	200	0.756	900	400	18.9
X3.Penten.2.one	3.584951	0	0	0	0	0	0	200	200	0.456	400	200	7.78
X1.Hexene..4.5.dimethyl.	5.972391	0	0	0	40	40	0.116	50	50	0.0981	300	200	6.61
X1.Butanol..2.3.dimethyl.	6.381056	100	100	0.0593	0	0	0	500	500	0.984	100	70	3.11
Furan..tetrahydro.2.2.5.5.tetramethyl.	9.380384	0	0	0	100	50	0.287	0	0	0	80	80	1.81
X2.Hexene..3.5.5.trimethyl.	9.510063	100	100	0.0613	40	40	0.0993	80	80	0.149	0	0	0
Formic.acid..2.methylbutyl.ester	9.511468	0	0	0	30	30	0.0873	50	50	0.0861	0	0	0
X1.Octen.3.ol *	9.604704	100,000	9,000	47.5	20,000	4,000	59.6	40,000	7,000	72.4	0	0	0
Glycidol	9.912637	300	300	0.119	100	60	0.298	500	300	0.984	600	200	13.2
X1.Octanol *	11.185791	1,000	200	0.592	300	60	0.735	400	60	0.825	0	0	0
X5.Hydroxy.7.methoxy.2.methyl.3.phenyl.4.chromenone	12.466348	400	200	0.182	70	70	0.187	200	100	0.394	80	80	1.71
X2.Oxo.4.phenyl.6..4.chlorophenyl..1.2.dihydropyrimidine	12.467318	30,000	30,000	13.3	0	0	0	60	60	0.118	90	90	1.99
Nonanoic.acid	14.204481	40,000	40,000	17.2	7,000	7,000	20.9	800	800	1.55	200	200	3.43
Decane..3.ethyl.3.methyl.	14.410620	90	90	0.0389	30	30	0.0970	0	0	0	0	0	0
Dodecane..4.6.dimethyl.	14.411667	700	700	0.281	5,000	5,000	14.0	300	300	0.503	300	300	5.50
Undecanal	14.793859	0	0	0	0	0	0	70	70	0.133	70	70	1.48
Carbonic.acid..decyl.undecyl.ester	14.794790	80	80	0.0351	50	30	0.150	40	40	0.0760	0	0	0
Propanoic.acid..2.methyl...3.hydroxy.2.2.4.trimethylpentyl.ester	15.772135	80	80	0.0351	20	20	0.0558	40	40	0.0760	0	0	0
Z.2.Dodecenol	16.171815	0	0	0	0	0	0	40	40	0.0693	50	50	1.04
Undecane..4.7.dimethyl.	16.553371	200	200	0.0706	90	50	0.256	600	500	1.19	400	200	9.24
Tridecane	16.553396	70	70	0.0292	0	0	0	30	30	0.0605	0	0	0
Decyl.octyl.ether	16.709269	300	300	0.144	80	40	0.229	40	40	0.0745	0	0	0
Dodecane..1.iodo.	16.737946	0	0	0	0	0	0	90	2	0.169	70	40	1.51
X2.4.Di.tert.butylphenol	17.486848	1,000	1,000	0.472	30	30	0.0873	9,000	8,000	17.7	0	0	0
Pentanoic.acid..5.hydroxy...2.4.di.t.butylphenyl.esters	17.487625	2,000	300	0.845	500	100	1.45	500	200	0.852	700	100	15.2
Hexane..3.3.dimethyl.	17.801547	0	0	0	90	50	0.248	40	40	0.0706	50	50	1.08
Undecane..4.6.dimethyl.	17.866389	0	0	0	70	70	0.197	0	0	0	50	50	1.14
Hexadecane	18.449101	200	100	0.0922	200	40	0.475	40	40	0.0746	50	50	1.05
X1H.Indene..2.3.dihydro.1.1.3.trimethyl.3.phenyl.	19.665437	40,000	40,000	17.8	50	30	0.146	70	30	0.127	90	50	1.97

¹ Confirmed and tentative identifications based on NIST14 library spectra and uafR structural references to public repositories.

² Asterisks indicate compounds are confirmed with commercial standards purchased from MilliporeSigma.

³ Zero emissions represent cases where volatiles were below the detection threshold.

⁴ Emissions rate are represented in ng per g of dry biomass.

Video-tracking Assay with Ethovision

The movement by *P. japonica* to the control and treatment extracts were similar for all response variables (distance, velocity, frequency, cumulative duration and latency; Appendix A, Table A.3) Estimated marginal means from GLMMs also indicated no statistical differences between treatments. While contrasts for cumulative duration in treatment half were not significant (all $p > 0.3$, Figure 5a), numerically the longest time spent by *P. japonica* was in monoculture soy (0.1531 ± 0.249), followed by an intermediate duration in intercropped soy (0.007 ± 0.249), and the shortest duration spent in the soy-sorghum mix (-0.311 ± 0.249). For frequency of entries into the treatment stimulus zone, there was slightly higher frequency of entries in monoculture soy (emmean $\pm$ SE) (0.2541 ± 0.288), intermediate entries in intercropped soy (0.0573 ± 0.307), and lower frequency of entries in the soy-sorghum mix (-0.0413 ± 0.316), but contrasts between treatments were not significant (all $p > 0.5$, Figure 5b). *Popoillia japonica* individuals had near equal latency for arrival to the stimulus zone (all $p > 0.9$, Figure 5c) whether it was monoculture soy (5.21 ± 0.214), intercropped soy (5.25 ± 0.274), and the soy-sorghum mix (5.28 ± 0.274). For mobility, there was numerically higher mobility in monoculture soy with 2–3-fold more mobility than the intercropped soy and the soy-sorghum mix, but contrasts between treatments were not significant (all $p > 0.6$, Figure 5d).

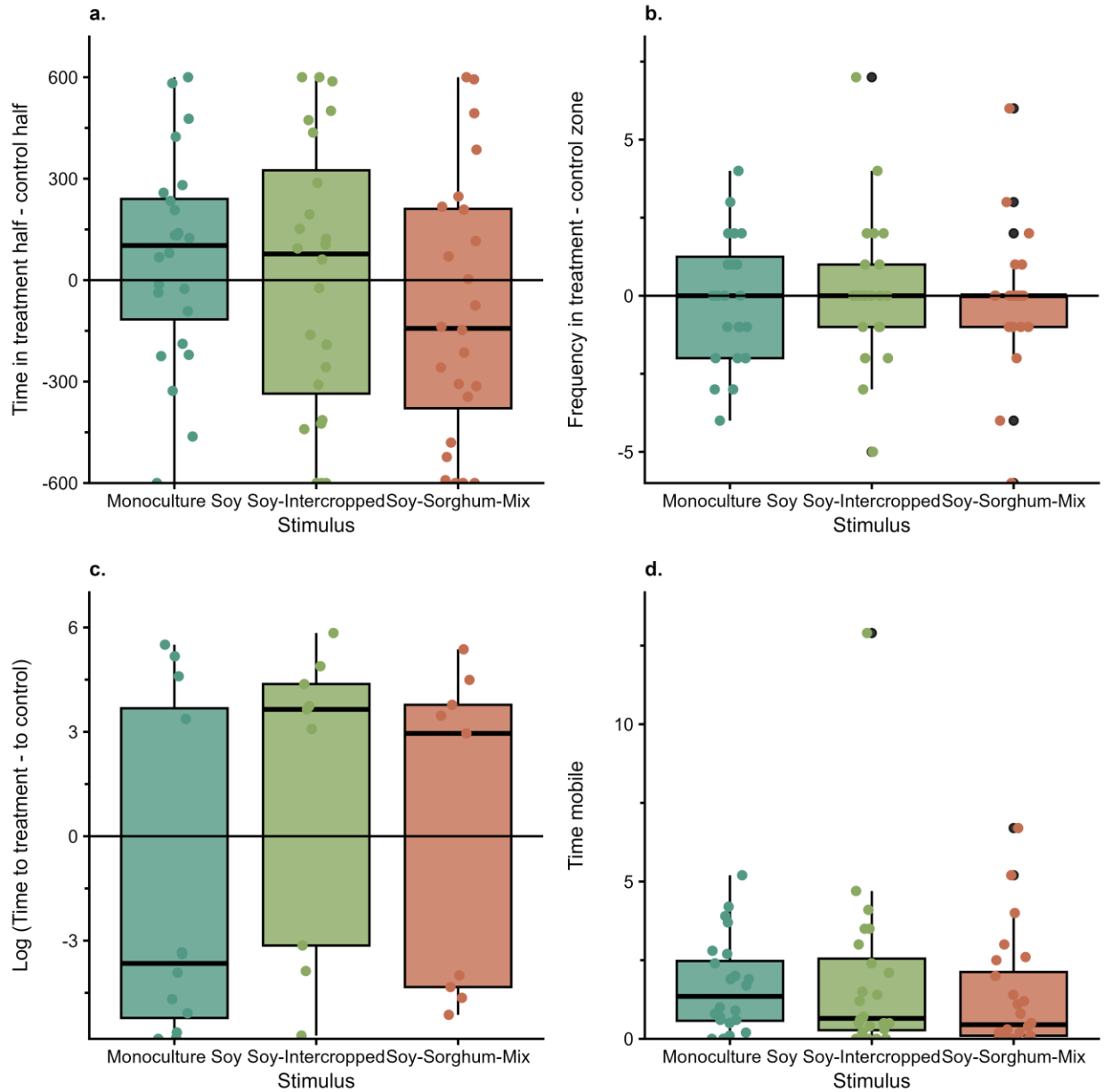


Figure 4-5 Comparisons of *P. japonica* behaviors within video-tracking assays shown as the difference between treatment and control values (log values for latency). Behaviors include (a), frequency of entries into the treatment stimulus zone (b), latency to finding the treatment stimulus zone (c), and mobility (d). Points indicate individual responses, center lines represent group medians, boxes represent interquartile ranges, and black dots indicate outliers. Abbreviations: mono soy = monocropped soy, inter soy = intercropped soy, mix= soy-sorghum-mix.

Preference Assay

After 1 h, the locations of beetles in the dual-choice assay did not indicate an initial preference for any treatment (Figure 6a, Table 3). Response rates ranged from 57% to 75%, which is a sufficient recapture rate for reasonable inference. In monosoy versus intersoy arenas, 33% more individuals chose intersoy than monosoy. In monosoy versus mix arenas, 37% more individuals chose mix than monosoy. In monosoy versus sorghum arenas, 66% more individuals chose sorghum than monosoy. In intersoy versus mix arenas, 66% more individuals chose mix than intersoy. Pairwise comparisons confirmed that there was no significant detectable preference in any of the dual choice assays after 1 h ($P > 0.2$; Table 3).

Similarly, after 24 h, the locations of beetles in the dual-choice assay did not indicate a final preference for any treatment zone (Figure 6b, Table 3). In monosoy versus intersoy arenas, 10% more individuals chose intersoy than monosoy. In monosoy versus mix arenas, 83% more individuals chose mix than monosoy. In monosoy versus sorghum arenas, 43% more individuals chose monosoy than sorghum. In intersoy versus mix arenas, individuals were equally divided between intersoy and mix. Pairwise comparisons confirmed that there was no significant detectable preference in any of the dual choice assays after 24 h ($P > 0.3$, Table 3).



Figure 4-6 Proportion of beetles (n=28) found in each zone between two treatments found on opposite ends of a release-recapture dual choice assay after 1 h (a) and 24 h (b). Zones 1 and 5 included the treatment plants, while zones 2 and 4 indicate preference for either treatment. NR values indicate the rate of non-responders. Beetles who stayed in the center release zone (zone 3) or buried themselves in the peat moss were considered non-responders.

Table 4-3 Summary of the emmeans pairwise contrasts for comparing treatment preference in the release-recapture dual-choice assay for *Popillia japonica*.

TREATMENT	1 h			24 h		
	ODDS RATIO	SE	P	ODDS RATIO	SE	P
Monoculture Soy v. Intercropped Soy						
Monoculture Soy v. Intercropped Soy	1.6	0.88	0.69	1.2	0.66	0.96
Intercropped Soy v. No Choice	2.2	1.3	0.34	1.2	0.66	0.96
Monoculture Soy v. No Choice	1.4	0.85	0.82	1.0	0.57	1.0
Monoculture Soy v. Soy-Sorghum-Mix						
Monoculture Soy v. Soy-Sorghum-Mix	1.6	0.92	0.68	1.7	1.1	0.64
Soy-Sorghum-Mix v. No Choice	1.4	0.76	0.84	0.73	0.41	0.84
Monoculture Soy v. No Choice	1.8	0.49	0.96	0.42	0.25	0.32
Monoculture Soy v. Sorghum						
Monoculture Soy v. Sorghum	0.49	0.30	0.47	1.7	0.98	0.66
Monoculture Soy v. No Choice	0.36	0.22	0.21	0.86	0.47	0.96
No Choice v. Sorghum	1.4	0.74	0.85	1.9	1.1	0.49
Intercropped Soy v. Soy-Sorghum-Mix						
Intercropped Soy v. Soy-Sorghum-Mix	0.49	0.30	0.47	1.0	0.56	1.0
Intercropped Soy v. No Choice	0.36	0.22	0.21	1.4	0.80	0.84
Soy-Sorghum-Mix v. No Choice	0.74	0.41	0.85	1.4	0.80	0.84

Discussion

In this study, we have investigated whether the mechanism for abundance shifts by *P. japonica* in intercropped soybeans compared to monocropped noted by Holmes and Barrett (1997) and Bohlen and Barrett (1990) arose because of semiochemical differences in plants or patches. While we found that monocropped soybean had highly unique emissions compared to intercropped soybean or sorghum, we did not find support for the hypothesis that *P. japonica* responded differently to semiochemicals from these plants on a localized scale. Furthermore, we found that groups of *P. japonica* showed no preference to leaves of any treatment within a release-recapture assay 1 or 24 h. Overall, this suggests that if the pattern of lower abundance by *P. japonica* in intercropped soybean is in fact true, there may be an alternative mechanism, such as mediation through visual stimuli or abiotic factors, due to the hierarchical nature of foraging decisions (Andersson et al. 2013).

We did indeed find significant and unique semiochemicals in the monocropped soybean extracts compared to intercropped soybean or sorghum, supporting our first hypothesis that intercropping soybean with sorghum could change the semiochemical profile of the intercropped soybean due to interactions with the neighboring sorghum plants. The main compounds found in monocropped soybean were 1-octen-3-ol and nonanoic acid. Previous studies have consistently identified 1-octen-3-ol as one of the most abundant compounds in soybean volatiles (del Rosario et al. 1984, Damiani et al. 2000, Boué et al. 2003, Cai et al. 2015). Rosario et al (1984) found that 1-octen-3-ol was present in soybeans (*Glycine max*), but not winged beans (*Psophocarpus tetragonolobus*). In our analysis, 1-octen-3-ol was identified as an indicator species for

monocropped soybean and the soybean-sorghum-mixture, but not intercropped soybean or sorghum. Abundances of this compound in intercropped soybean were much lower, and it was completely absent from sorghum. The semiochemical profile of monocropped soybeans also contained 1-octanol at levels more than 3-fold higher than intercropped soybeans. A previous study on the response of *P. japonica* to maple species similarly found susceptible maples emitted fruity-smelling esters, whereas resistant species emitted terpene hydrocarbons (Loughrin et al. 1997). The aroma of 1-octanol has notes of rose (Moore 2022), a host for which *P. japonica* have a strong preference (Whittington et al. 1942). Intercropping soybean with sorghum reduced the levels of one of the key semiochemical components identifying soybean (1-octen-3-ol), as well as 1-octanol which may have a preferred aroma to *P. japonica* within the intercropped soybean leaves compared to monocropped soybean leaves. The differences in the amount of these two compounds could possibly result in variation in the olfactory responses by *P. japonica*.

However, despite significant differences among the semiochemical profiles in each treatment, there was no behavioral difference to support any preference on a local scale for any treatment or extract by *P. japonica*. These results suggest that olfactory cues likely do not mediate this behavior pattern in the field; decisions may be mediated by visual cues at a broader scale. If volatiles are involved, it could be that responses occur at a different scale, or during flight in the field. It does not appear that host cues are important at a local level. Plume reach of host volatiles varies by species (Kirkpatrick et al. 2019, Agrafioti et al. 2025) and the presence or absence of host plants (Kirkpatrick et al. 2019). A study of *P. japonica* distribution around an airport found that agricultural host plants within 500 m of the traps were consistently positively correlated with higher trap catches (Hamilton et al. 2007). Work with other invasive species has found host cues can have an arrestment function at a local level (Morrison et al. 2016), but we

found no evidence for arrestment by *P. japonica* during the video-tracking assay in our study. Overall, behavioral differences by *P. japonica* to intercropped soybean and monocropped soybean were minimal.

Earlier field studies by Holmes & Barrett (1997) and Bohlen & Barrett (1990) suggested that sorghum strips created a barrier to movement, and therefore reduced abundance of *P. japonica*. Specifically, the authors found fewer marked *P. japonica* traveled to the center of intercropped soybean fields compared to the monocropped fields. Sorghum is not one of *P. japonica*'s 300 preferred hosts (APHIS 2022), and perhaps its presence deters *P. japonica* from the intercropped soybean fields. If this were the case, we would expect to see a preference for monocropped soybean compared to sorghum in our two-choice release-recapture assays with fresh leaves. However, within the release-recapture assays, no preference was shown for monocropped over intercropped soybean, a mixture of soybean and sorghum, or sorghum alone. This is similar to previous findings by Loughrin et al. (1997) with *P. japonica*-susceptible and -resistant maples. Numbers of *P. japonica* recaptured in the sorghum zones and monocropped soybean zones did not differ significantly, and we observed individuals feeding on both sorghum leaves and flowers (pers. obs. N. Kuchеров). Assays were analyzed after 1 h and 24 h periods, allowing us to determine if the presence of *P. japonica* and feeding damage on preferred leaves would recruit conspecifics to the same side in the arena. Previous studies have found that host plants are more attractive to *P. japonica* after overnight feeding (Loughrin et al. 1995, 1996). Therefore, we expected *P. japonica* to show a stronger preference after 24 h. Surprisingly, recapture results at 24 h still showed no preference for any treatment and feeding damage was indistinguishable across treatments. This suggests that *P. japonica* are not repelled from mixes of sorghum and soybean, or even sorghum alone at a local scale. Any preferences for soybean over

sorghum at a field scale may also be related to microclimate variables such as temperature and relative humidity rather than olfactory or visual attractiveness of the leaves.

Popillia japonica are known to disperse and forage across long distances (Lessio et al. 2021), and many studies have shown that their presence and abundance is related to landscape composition (Hamilton et al. 2007, Della Rocca and Milanesi 2022, Henden and Guédot 2022, Kucherov et al. 2025). They also exhibit spatial aggregation and are found in higher densities at field edges (Sara et al. 2013, Henden and Guédot 2022), prefer direct sunlight and are mostly found within the top third of the canopy of host plants (Rowe and Potter 1996, Shanovich et al. 2019, Toninato et al. 2024). Even though they are often found in areas receiving direct sunlight, they may have microhabitat preferences as high proportions are found in shaded microsites such as the undersides of leaves (Kreuger and Potter 2001). Although much of the literature on *P. japonica* focuses on their olfactory responses, they also use visual cues such as color and light intensity (Guignard et al. 2025). It has also been suggested that they may orient to visually to silhouettes of host plants (Rowe and Potter 1996). Host orientation in response to visual stimuli in silhouette form has been demonstrated in other beetles such as weevils (Hausmann et al. 2004, Machial et al. 2012), ambrosia beetles (Mayfield and Brownie 2013), bark beetles (Strom and Goyer 2001), lady beetles (Nalepa et al. 2005), and stink bugs (Leskey et al. 2012). It is possible that *P. japonica* make foraging decisions in a hierarchical manner, for example locating fields at a broad scale first by visually identifying the size of a patch of host plants (Andersson et al. 2013), and then utilizing different sensory cues at a finer scale such as abiotic cues from the microclimate or gustatory cues (Verschut et al. 2017). Thus, it may be possible that the unique silhouette of sorghum in the landscape compared to soybean may be a repellent stimulus, but we

did not explicitly test this. However, it appears there was no behavioral evidence for use of olfactory cues by *P. japonica* on a local scale in intercropped systems.

A potential management implication is that intercropping soybean with sorghum may not be a preferred option for deterring *P. japonica*, especially in areas where *P. japonica* could be entering from a bordering field or woodlot. Our results suggest that *P. japonica* may not be deterred from intercropped soybean and sorghum fields through a host-plant semiochemically-mediated mechanism, at least not at the local scale. Another, more successful option for mitigating *P. japonica* damage may be choosing a soybean variety that is more resistant to *P. japonica* (Shanovich et al. 2019, Menger et al. 2023).

Future work could include investigating visual cues used by *P. japonica* or the influencing of landscape configuration on abundance. Orientation to preferred host plants by *P. japonica* may occur through other mechanisms such as visual or landscape cues, or across different spatial or temporal scales. Changes in the movement of *P. japonica* into the intercropped soybean fields could be due to the presence of edges induced by intercropping, including differences in microclimates, rather than the particular presence of sorghum itself. Therefore, future studies could investigate the effects of different field borders on the movement of *P. japonica* into soybean fields. Nevertheless, this work significantly contributes to our knowledge of host selection by *P. japonica*. We show that in close proximity, *P. japonica* acts as a true generalist, equally attracted to preferred and not preferred host plants. We also show that intercropped soybeans have unique a semiochemical composition separate from monocropped soybean, although those differences did not produce any variation in *P. japonica* behavior.

Chapter 5 - Conclusion

Insect communities change across landscapes and over time in response to fluctuations in temperature, precipitation, and the availability of resources such as food and habitat. Therefore, we can expect insect communities in agricultural fields to change throughout space and time in predictable ways depending on their local climate conditions and surrounding landscape. One goal of this research was to disentangle and identify the effects of land cover and climate variables on agricultural insect communities. To better understand how agriculturally important insects respond to each of these variables, we need to consider all of these variables.

Natural land in agricultural landscapes: a help, not a hindrance

Previous studies have shown inconsistent effects of semi-natural land cover in the surrounding landscape on the abundance of pests and predators or the predation rates in agricultural fields (Chaplin-Kramer et al. 2011, Veres et al. 2013, Karp et al. 2018). Because these studies spanned multiple years and large geographic areas, spatial and temporal climatic variation may account for some of the inconsistency. We sought to identify possible interactions between seasonal precipitation and seminatural land cover in the surrounding landscape that significantly affect the abundance or community composition of insect pests, predators, and pollinators in soybean fields through a carefully designed field study across eastern Kansas that spanned a large gradient of semi-natural land cover within three separate precipitation bands. We were able to identify a significant effect of the interaction between surrounding grassland or semi-natural land and seasonal precipitation on the abundance of insect predators and pollinators in soybean fields.

Our first study provides evidence that precipitation interacts with the effects of land cover, masking or minimizing the effects of land cover on beneficial insect populations at lower precipitation levels. The amount of surrounding grassland had a negative effect on insect pest abundance. Predator abundance also had a negative relationship with increasing surrounding grassland, possibly tracking pest abundance. However, the magnitude of the land cover effects varied with precipitation for predators and pollinators. Pollinator abundance increased with increasing natural land cover, but the response was strong in areas of high precipitation and weaker in areas of low precipitation. Preserving or restoring natural lands may result in lower pest pressure and high pollination rates in agricultural fields because increasing the proportion of grassland or semi-natural land in the landscape surrounding our soybean fields reduced the abundance of key pests and increased pollinator abundance, respectively. Importantly, these relationships may be masked or minimized under low precipitation conditions, and therefore it is necessary to consider the interaction between precipitation and land cover in future studies and management.

Restoring sections of semi-natural habitat and increasing plant diversity supports a wider variety of natural enemies and pollinators in agroecosystems (Egan et al. 2020, Lundin 2021). We found that the dominant groups of natural predator communities change in response to seasonal climate variables, and therefore it is imperative to support a diverse community of natural predators within agricultural fields, especially as seasonal weather becomes less predictable. Contrastingly, pollinator communities are mainly driven by the proportion of surrounding semi-natural land, and adding prairie strips or conservation land into our

agroecosystems is important for supporting our bee-dominated pollinator communities. As such, interannual variation in precipitation and temperature could lead to communities dominated by different pests, different predators, and different pollinators within the same location. To buffer against the loss of key natural predators and pollinators due to climatic changes, it is therefore important to support diverse communities of beneficial insects.

***Popillia japonica*: a turf pest, not a grassland pest**

One concerning agricultural pest currently is the Japanese beetle, *Popillia japonica* Newman. *P. japonica* is an invasive agricultural pest currently spreading throughout the Great Plains. Known as a particularly destructive pest of turf grass, it was predicted that the grasslands and pastures of the Great Plains would support a greater abundance of *P. japonica* larvae, leading to an increased threat to important field crops such as soybean and corn in this area (Kistner-Thomas 2019). However, existing risk maps for Japanese beetles in the United States did not include land cover variables (Zhu et al. 2017, Kistner-Thomas 2019). Furthermore, existing risk maps did not incorporate a temporal aspect even though many currently unoccupied areas are likely to be suitable but not yet reached at this time.

To fill these gaps, my second study explored the effects of regional land cover alongside climate factors within counties with, and without, *P. japonica* present over a five year period, allowing us to identify relationships between environmental and climatic factors and *P. japonica* presence and predict *P. japonica* into the near future and under future climatic conditions. Probability of *P. japonica* presence increased sharply with increasing developed area within a county, probably due to the abundance of turf in lawns and communal recreational areas within developed areas available for the development of their larvae. The proportion of soybean and

corn within each county was also positively related to *P. japonica* presence. Climate variables also had significant effects; probability of *P. japonica* presence was low in areas with the lowest temperature minimums and highest temperature maximums and increased with increasing precipitation until an annual precipitation amount of approximately 1000mm.

Despite predictions to the contrary, we found that grasslands and pastures had a significant negative relationship with *P. japonica* presence in the Midwest and Great Plains. Although *P. japonica* are pests of turfgrass, and native grasslands are also grasses, there are many biologically important differences which may account for this unexpected relationship. Grasslands in the Great Plains have distinct species with different heights and management practices compared turf grass or grasslands in the eastern United States Tallgrass prairies of the Midwest and Great Plains have characteristically tall, dense, stands of grass with deep root systems (Weaver and Fitzpatrick 1932) which may be unpalatable *P. japonica* grubs. Additionally, grasslands support native bird species which have been known to prey on *P. japonica* adults (Fleming 1968).

Understanding how landscape effects insect communities in agricultural fields, and the spread of invasive species can be very helpful for use within decision tools for tracking invasive species spread or forecasting pest abundance to inform surveillance and management practices. If possible, planting strips of grassland or restoring sections to prairie within the landscape would be beneficial for reducing pest populations and supporting pollinator populations in nearby fields. Unfortunately, stakeholders cannot always change the land around their agricultural fields. Therefore, we looked at plant-insect interactions on a local scale to evaluate the behavioral mechanism of the recommended practice of intercropping soybean with sorghum that may help to reduce the number of *P. japonica* within a soybean field.

If there is a behavioral response by *P. japonica* in the field to intercropping sorghum with soybean, it may arise from confusion due to different olfactory cues. *P. japonica* are attracted to various semiochemical cues including conspecific pheromones (Tumlinson et al. 1977, Klein et al. 1981), and host plant compounds (Ahmad 1982, Loughrin et al. 1995, 1998). In our third study, we investigated a semiochemical-based mechanism for the behavioral response of *P. japonica* to intercropping soybean with sorghum through characterization of the semiochemical profiles of monocropped soy, intercropped soy, and a mixture of soy and sorghum through solid phase microextraction (SPME) in conjunction with gas chromatography coupled with mass spectrometry (GC-MS), and evaluation of *P. japonica* behavioral response through video-tracking of movement with semiochemical extracts and preference in a release-recapture dual choice assay to host stimuli from plants. Although we found unique semiochemical profiles among our treatments, movement or orientation by *P. japonica* was not significantly different between treatment extracts and controls, nor did they show a significant preference for any of the treatments in a dual choice assay at a local scale. Therefore, we concluded that if intercropping soybean with sorghum significantly affects the behavior of *P. japonica* in the field, it must occur at a different scale, or in response to non-olfactory stimuli (e.g., visual, habitat, or landscape cues) rather than semiochemical cues.

Agricultural insect communities in changing landscapes and climates

Overall, our work shows that agriculture insect communities are responding to environmental factors at various scales which are often larger than a single field. Additionally, variations in climate significantly affect insect abundance and community composition. For beneficial insects, there is also an interaction between climate and land cover variables which

should be considered in future studies and will become even more important with predicted changes to temperature and precipitation patterns. As we are rethinking how we manage the world's agricultural land, it is imperative that we look at the land from an ecological perspective. Agricultural fields are not closed systems, they exist within a landscape which both affects and is affected by the management choices within that field. Landscape simplification reduces supportive resources for beneficial insects, leading to an increased need for pesticides, then pesticides further reduce the populations of beneficial insects, often leading to secondary pest outbreaks.

As climate changes and global trade increases, we are seeing range expansions of invasive agricultural pests, and this is a growing concern. To adequately predict, track, and monitor invasive species we need to consider their interactions with land cover and climatic variables across multiple scales. While global risk maps based on climate variables are valuable, regional scales must consider unique local land cover variables. An invasive species current realized niche is likely not its fundamental niche, and predictions based on dissimilar regions may not be accurate. Furthermore, land cover classes do not cover the full range of ecosystem variation, and insects may not response equally to one land cover across geographic regions. Risk maps should be developed at regional and local scales to accurately predict invasions and infestations, and they should include both climate and land cover variables, to respond to the increasing risks of invasive species efficiently.

Our research was conducted mainly in soybean within a temperate grassland ecosystem and therefore may not be generalizable to other systems. It will be important to replicate our findings within different agricultural systems and natural environments. Future studies could also test the most effective landscape configurations for adding semi-natural areas to increase

predation and pollination within agricultural fields. Perhaps more challenging future work includes developing effective strategies for supporting landscape scale management strategies as a society and at community levels. We will need to work together as communities to address land-scape level pests at the appropriate scale.

References

- Ahmad, S. 1982. Host location by the Japanese beetle: Evidence for a key role for olfaction in a highly polyphagous insect. *Journal of Experimental Zoology* 220:117–120.
- Chaplin-Kramer, R., M. E. O’Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters* 14:922–932.
- Egan, P. A., L. V. Dicks, H. M. T. Hokkanen, and J. A. Stenberg. 2020. Delivering Integrated Pest and Pollinator Management (IPPM). *Trends in Plant Science* 25:577–589.
- Fleming, W. E. 1968. Biological Control of the Japanese Beetle. Technical Bulletins.
- Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, L. Hunt, A. E. Larsen, A. Martínez-Salinas, M. E. O’Rourke, A. Rusch, K. Poveda, M. Jonsson, J. A. Rosenheim, N. A. Schellhorn, T. Tscharntke, S. D. Wratten, W. Zhang, A. L. Iverson, L. S. Adler, M. Albrecht, A. Alignier, G. M. Angelella, M. Zubair Anjum, J. Avelino, P. Batáry, J. M. Baveco, F. J. J. A. Bianchi, K. Birkhofer, E. W. Bohnenblust, R. Bommarco, M. J. Brewer, B. Caballero-López, Y. Carrière, L. G. Carvalheiro, L. Cayuela, M. Centrella, A. Četković, D. C. Henri, A. Chabert, A. C. Costamagna, A. De la Mora, J. de Kraker, N. Desneux, E. Diehl, T. Diekötter, C. F. Dormann, J. O. Eckberg, M. H. Entling, D. Fiedler, P. Franck, F. J. Frank van Veen, T. Frank, V. Gagic, M. P. D. Garratt, A. Getachew, D. J. Gonthier, P. B. Goodell, I. Graziosi, R. L. Groves, G. M. Gurr, Z. Hajian-Forooshani, G. E. Heimpel, J. D. Herrmann, A. S. Huseth, D. J. Inclán, A. J. Ingrao, P. Iv, K. Jacot, G. A. Johnson, L. Jones, M. Kaiser, J. M. Kaser, T. Keasar, T. N. Kim, M. Kishinevsky, D. A. Landis, B. Lavandero, C. Lavigne, A. Le Ralec, D. Lemessa, D. K. Letourneau, H. Liere, Y. Lu, Y. Lubin, T. Luttermoser, B. Maas, K. Mace, F. Madeira, V. Mader, A. M. Cortesero, L. Marini, E. Martinez, H. M. Martinson, P. Menozzi, M. G. E. Mitchell, T. Miyashita, G. A. R. Molina, M. A. Molina-Montenegro, M. E. O’Neal, I. Opatovsky, S. Ortiz-Martinez, M. Nash, Ö. Östman, A. Ouin, D. Pak, D. Paredes, S. Parsa, H. Parry, R. Perez-Alvarez, D. J. Perović, J. A. Peterson, S. Petit, S. M. Philpott, M. Plantegenest, M. Plečáš, T. Pluess, X. Pons, S. G.

- Potts, R. F. Pywell, D. W. Ragsdale, T. A. Rand, L. Raymond, B. Ricci, C. Sargent, J.-P. Sarthou, J. Saulais, J. Schäckermann, N. P. Schmidt, G. Schneider, C. Schüepp, F. S. Sivakoff, H. G. Smith, K. Stack Whitney, S. Stutz, Z. Szendrei, M. B. Takada, H. Taki, G. Tamburini, L. J. Thomson, Y. Tricault, N. Tsafack, M. Tschumi, M. Valantin-Morison, M. Van Trinh, W. van der Werf, K. T. Vierling, B. P. Werling, J. B. Wickens, V. J. Wickens, B. A. Woodcock, K. Wyckhuys, H. Xiao, M. Yasuda, A. Yoshioka, and Y. Zou. 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences* 115:E7863–E7870.
- Kistner-Thomas, E. J. 2019. The potential global distribution and voltinism of the Japanese beetle (Coleoptera: Scarabaeidae) under current and future climates. *Journal of Insect Science* 19:16.
- Klein, M. G., J. H. Tumlinson, T. L. Ladd, and R. E. Doolittle. 1981. Japanese beetle (Coleoptera: Scarabaeidae) : Response to synthetic sex attractant plus phenethyl propionate: Eugenol. *Journal of Chemical Ecology* 7:1–7.
- Loughrin, J. H., D. A. Potter, and T. R. Hamilton-Kemp. 1995. Volatile compounds induced by herbivory act as aggregation kairomones for the Japanese beetle (*Popillia japonica* Newman). *Journal of Chemical Ecology* 21:1457–1467.
- Loughrin, J. H., D. A. Potter, and T. R. Hamilton-Kemp. 1998. Attraction of Japanese Beetles (Coleoptera: Scarabaeidae) to Host Plant Volatiles in Field Trapping Experiments. *Environmental Entomology* 27:395–400.
- Lundin. 2021. Integrated pest and pollinator management – expanding the concept. *Frontiers in Ecology and the Environment*.
- Tumlinson, J. H., M. G. Klein, R. E. Doolittle, T. L. Ladd, and A. T. Proveaux. 1977. Identification of the Female Japanese Beetle Sex Pheromone: Inhibition of Male Response by an Enantiomer. *Science* 197:789–792.
- Veres, A., S. Petit, C. Conord, and C. Lavigne. 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agriculture, Ecosystems & Environment* 166:110–117.
- Weaver, J. E., and T. J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of Tall-Grass Prairie. *Botanical Gazette* 93:113–150.
- Zhu, G., H. Li, and L. Zhao. 2017. Incorporating anthropogenic variables into ecological niche modeling to predict areas of invasion of *Popillia japonica*. *Journal of Pest Science* 90:151–160.

Appendix A -

Table A.1: Insect Totals. Insects are identified as pests in red, predators in green, pollinators in blue, and other insects in black. Thrips and whiteflies were not counted as pests due to correlation with leaves in the sweep.

BeanLeafBeetle	2176
CornRootWorm	557
BlisterBeetles	35
DectesStemborer	453
JapaneseBeetles	1464
LeafFrogHoppers	3275
FleaBeetle	285
HerbivorousStinkBugs	409
Chloropid	1156
Lepidoptera	282
Aphids	350
GrasshoppersCrickets	966
OtherHemiptera	1567
PlantBug	407
Caterpillars	658
GreenWorms	875
PredatoryStinkbugs	104
MinutePirateBug	2270
LongLeggedFlies	994
ParasiticWasps	2299
OtherWasps	357
Ants	530

Lacewings	106
Ladybugs	57
ReduviidaeNabidae	175
Spiders	5655
HoneyBee	226
BumbleBee	35
LgCarpenter	19
LongHornedBees	4
SweatBees	162
Megachilidae	34
Andrenidae	2
HoverFlies	65
MidgesMosquitos	2504
BlackFlies	13020
Thrips	25974
Whiteflies	34152
OtherDiptera	3584
OtherBeetles	1215
Springtails	168

Table A.2: Results from the interaction generalized linear mixed-effects model for evaluating the effects of semi-natural land cover (proportion grassland), seasonal precipitation, ecoregion (Glaciated or Cuestas relative to Flint Hills), local edge type (agricultural, road, or semi-natural), and summer maximum temperature on pest abundance. All fixed-effect predictors included in the full models are shown; the random effect of site is not displayed. Significant effects are identified in bold font.

Variable	Pest estimate- interactive model
Land cover and precipitation interaction	-0.110 ± 0.061 (p = 0.07)
Grass or semi-natural land cover	-0.198 ± 0.071 (p < 0.01)
Seasonal Precipitation	-0.083 ± 0.083 (p = 0.32)
Summer Average Maximum Temperature	-0.030 ± 0.061 (p = 0.77)
Agricultural Edge	0.504 ± 0.110 (p < 0.001)
Road Edge	0.327 ± 0.092 (p < 0.001)
Semi-Natural Edge	0.227 ± 0.101 (p = 0.06)
Ecoregion- Osage Cuestas	0.121 ± 0.144
Ecoregion- Glaciated	0.369 ± 0.163

Table A.3: Summary of the t-tests for the preference index comparing the control to the treatment in the video-tracking assay coupled with Ethovision for *Popillia japonica*.

Treatment	MEAN	T	P
Frequency in each arena half			
Monoculture Soy	0.0060	0.090	0.93
Intercropped Soy	-0.040	0.46	0.65
Soy-Sorghum-Mix	-0.11	1.2	0.23
Frequency in stimulus zone			
Monoculture Soy	0.066	0.41	0.69
Intercropped Soy	-0.090	-0.54	0.60
Soy-Sorghum-Mix	-0.080	-0.44	0.67
Cumulative duration in each arena half			
Monoculture Soy	0.11	1.0	0.31
Intercropped Soy	0.010	0.10	0.92
Soy-Sorghum-Mix	-0.16	-1.2	0.25
Cumulative Duration in stimulus zone			
Monoculture Soy	0.0040	1.5	0.16
Intercropped Soy	0.030	1.2	0.24
Soy-Sorghum-Mix	0.0020	0.66	0.52
Latency to each arena half			
Monoculture Soy	-0.010	-0.28	0.78
Intercropped Soy	0.040	1.3	0.20
Soy-Sorghum-Mix	0.010	0.19	0.85
Latency to stimulus zone			
Monoculture Soy	-0.11	-1.2	0.26
Intercropped Soy	0.050	0.54	0.60
Soy-Sorghum-Mix	-0.0010	-0.020	0.99