

Pushed over the edge: Insect communities at border habitats

by

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B.A., Luther College, 2020

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Department of Entomology
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2023

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Abstract

Increased agricultural intensification has had a profound impact on many ecological processes, including documented declines in beneficial insect abundance, richness, and their natural pest control services. With an increase in pest pressure, agrochemical use has also risen. Strategically planting perennial grassland habitat adjacent to working land, often called border cropping, is a practice that can work to counteract the negative impacts of intensification patterns and offer sustainable solutions for humans, insects, and our ecosystems long term. Border crops provide the additional shelter and food resources needed for beneficial insect survival, which boosts their abundances and diversity. Subsequently, if the beneficial insects move from the border crop into the agricultural field, they can provide natural pest control services needed to reduce pest pressure and agrochemical use. However, the effects of border crops for beneficial insects and pest control services have been mixed ranging from negative, no effect to positive effects. Mixed results have in large part been due to differences in response variables measured and different experimental approaches. Insect community patterns and spillover movement patterns within border crops and across agricultural landscapes remain relatively less well explored and must be studied more closely. It is possible that the beneficial insects are not moving between habitats, and thus have little impact on natural pest control, because the border crop's edge might be perceived as a barrier to movement.

My master's project works to understand insect movement between agricultural fields and their adjacent habitat types. It also focuses on gaining insight into the effectiveness of border crops as a natural pest control and a conservation practice. To achieve these goals, we conducted two studies across soybean plots that were bordered by either corn or grass natural habitats. One

was an observational biodiversity study and the other was an experimental mark, release, and recapture study. This two-part approach provided both a broader comprehensive view of insect dynamics and the intricate mechanistic patterns needed for scientific comprehension and agricultural management decisions. Results showed that it is likely that any edge habitat, including those created by border crops, are unique environments where they create separate communities and can be barriers to insect movement. We found that the overall pest and beneficial insect communities in soybeans were distinct from those at the edges and within the corn or grass interiors. We also found that movement between habitats was uncommon for tracked ground beetles, no matter the type of bordering habitats or type of edge. However, we also found positive indications for natural pest control with border crops. There were slightly more beneficial and less pest insects within soybean field interiors that had a border crop compared to soybean field interiors that had an adjacent corn habitat. In addition, tracked ground beetles most frequently chose to enter the soybean habitat over the grass or corn when placed at an edge. Therefore, with the implementation of various techniques, such as softening edges or using lures, border crop habitat edges could be more permeable, could promote cross habitat movement, and ultimately contribute to natural pest control.

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Acknowledgements

I want to thank Dr. Tania Kim for the amazing opportunity to pursue a graduate degree and to achieve my dream of becoming an entomologist. Her constant support, dedication, brilliance, mentorship, and guidance were transformative for this research and for my growth as a person, scientist, and future teacher. The past two years learning from Dr. Kim have been invaluable!

I want to thank Dr. Brian Spiesman, Dr. Brian McCornack, and Dr. Rachel Harman for their dynamic ideas and positive contributions to the project, which were highly valued. This research was not possible without them.

I also want to thank all the members of the Kim and Spiesman Lab Group. It was so fun working with this team! Thank you also to the local participating growers and collaborators. I really appreciated their trust in me and their belief in the importance of insect research. Thank you to my friends and colleagues in the Department of Entomology and the Popenoe Entomology Club. This was such a special community!

I also want to acknowledge the financial support from Kansas State University, The Department of Entomology, and the United States Department of Agriculture for making this research possible.

Finally, I want to thank my family. The unlimited and unwavering love, joy, and belief they provided each day over the past two years, and throughout my entire life, was the foundation to my happiness and success as a master's student.

Chapter 1 - General Introduction

1.1 INTRODUCTION

The immense demand for agricultural crop production in the United States and throughout the world has dramatically altered our landscapes and ecosystem functions (Spangler et al 2020; Dirzo et al 2014; Geiger et al 2011). We now live in a highly simplified environment characterized by great spans of single crop types, which have markedly replaced alternative crop varieties and other beneficial natural to semi-natural habitats (Meehan et al 2011; Gámez-Virués et al 2015). The number of acres of soybean and corn harvested has increased by 76% over the past 60 years while other crops have substantially declined (Spangler et al 2020). In addition, within the Midwest alone, two million hectares of grassland were converted to crops between 2008 and 2016 (Zhang et al 2021). As a result of this vast and low diversity cropping system, our landscapes have become severely depleted of essential natural resources, biotic contributors, and ecosystem services, including soil fertility, nutrient cycling, water and soil retention, decomposition, pollination, and natural pest control (Spangler et al 2020; Dirzo et al 2014; Grab et al 2018; Tschardt et al 2005). As a result, our landscapes cannot respond resiliently to disturbance (Oliver et al 2015).

A common solution to these ecological issues is to rely more heavily upon fertilizer, genetically engineered crops, chemical insecticides, and chemical pesticides (Matson et al 1997; Meehan et al 2011; Spangler et al 2020). The United States uses over a billion pounds of pesticides each year, many of which are banned in other countries because of their harmful target and non-target impacts (Donley 2019). This normalized solution is dangerous because it further depletes agriculture's essential natural resources, biotic contributors, and ecosystem services. It is especially disastrous for insects because it is a main driver of their dramatically significant

declines (Wagner 2020; Wagner et al 2021; Forister et al 2019; Dirzo et al 2014). Losing insects is tragic for agriculture because many insects provide beneficial services such as pollination, nutrients to crops, and dung removal (Forister et al 2019). Further, these helpful insects eat pests, which provides natural pest control that has been calculated to be worth around \$4.5 billion annually in the United States alone (Dirzo et al 2014). Without insects and their services, ecological issues within agricultural fields will continue to intensify, and the reliance on agrochemicals will continue. This ultimately creates a perpetual cycle of ecosystem weakening. An alternative solution to agrochemicals must be implemented to help maintain high quality yields for the growing global population while concurrently maintaining proper ecosystem functioning (Matson et al 1997). Ultimately, if we want food and economic stability moving forward, then we need diverse, resilient, and self-regulating ecosystems that are agrochemical independent, especially as climate change continues to increase environmental stressors and extremity with more frequent and severe fires, storms, and precipitation changes (Wagner et al 2021).

Creating structurally complex landscapes that contain greater diversities of land cover types interspersed into our current monocropping system is a conceivable strategy moving forward. Increasing the frequency of grassland, forest, or wetland natural habitats would provide for a wider abundance and richness of beneficial insects because there are more readily exploitable ecological opportunities. As a result of these natural habitats, the environment stabilizes and can respond resiliently to disease and disturbance (Tscharntke et al 2012; Tscharntke et al 2005; Landis 2017; Gardiner et al 2009; Jankielsohn 2018; Marja et al 2022; Oliver et al 2015). Border crops are a sustainable agricultural practice that works to achieve this desired goal of increased landscape complexity. Border crops are strategically planted permanent

and perennial natural habitats adjacent to agricultural fields. They can range from small strips of grassland to large fields of native flowering prairie. Often, these border crop plantings can be grazed, mowed, burned, or harvested in a methodical approach that coincides with the local conservation initiatives or in manners that work to mimic the historical landscape (Garibaldi et al 2021). It is well known that border crops will decrease water runoff, increase soil retention, and maintain nutrients, including the tremendously important nitrogen and phosphorus (Schulte et al 2017). Notably, a study conducted at the Neal Smith National Wildlife Refuge in Iowa, an establishment that works to restore native tallgrass prairie ecosystems, found that agricultural fields containing grassland had at least a 10 times reduction in soil loss and a 200% increase in plant species richness compared to agricultural fields without grassland (Liebman et al 2013). At that same refuge, there was significantly higher insect biodiversity within agricultural crop fields that had grass and floral presence (Schulte et al 2017). Therefore, in theory, a series of patches of small and low-maintenance border crop implementations across an extensive landscape of agricultural fields could easily accumulate to make an enormous impact towards restoring essential natural resources, biotic contributors, and ecosystem services.

Unfortunately, while these agronomic border crop benefits are well-documented and significant, their impact on beneficial insects and their natural pest control services is more complicated and variable. In theory, beneficial insect diversity and abundance should increase because the border crop provides landscape complexity, and thus the crucial and additional shelter, food, and resources needed for their survival (Grab et al 2018; Schulte et al 2017; Hopwood et al 2016; Landis et al 2000). In addition, pest populations would be expected to decrease due to those beneficial insects preying on them (Landis et al 2000; Bianchi et al 2006; Rand et al 2006; Liere et al 2015). Studies around the world have shown that within complex

landscapes, although not specifically border crops, these two trends are true. For example, a study conducted in Northwest China found greater natural enemy populations and lower cereal aphid pest populations within wheat fields that were part of a landscape that had greater diversity of habitat types (Zhao et al 2015). In addition, a regional study conducted across eight European countries found that both ground beetle species diversity and aphid predation increased as agricultural intensification decreased (Geiger et al 2011). Finally, a modeling study conducted across the Midwestern United States found that increased landscape complexity was correlated to less pest pressure and less insecticide use (Meehan et al 2011). Because border crops also increase landscape complexity, it would seem likely that they would also follow these trends. However, there is research that shows that increased landscape complexity from border crops can have little effect on pest abundance (Chaplin-Kramer et al 2011; Cox et al 2014) or it can even result in higher pest abundances (Fiedler and Landis 2007). In these cases, the lack of change in pest abundance could signify that despite the increase in landscape complexity from border crops, the beneficial insects are not actually predating within agricultural fields. Finding out why will be extremely important for maximizing the ecological potential of border crops (Rusch et al 2016).

A very probable reason for these variable findings is that an edge effect may be occurring at habitat boundaries and responses may vary from different animal groups including birds, mammals, and insects (Rand et al 2006; Ries et al 2004; Ries and Sisk 2004). A meta-analysis found there was greater probability of bird nest predation at forest edges (Vetter et al 2013). Another study found birds ate mantids most frequently and successfully at habitat edges (Ries and Sisk 2010). In addition, several studies have found significantly higher ground beetle abundances at edge habitats (French et al 2004; Rischen et al 2021; Magura et al 2017). This

information shows how habitat edges create unique environments with ecological impacts that vary from habitat interiors. Within agricultural landscapes, border crops create edges where the natural habitats meet the agricultural fields (Ries and Sisk 2004). These edge habitats are very likely impacting the insects and the ecosystem services that they provide for farmers. For border cropping to work, the beneficial insects, who naturally populate the natural habitats, must move across the edges into the agricultural fields where they can then prey upon pests. It is often assumed when implementing border crops that this cross-habitat movement is occurring because insects are highly mobile. Further, movement between agricultural habitats and natural areas has been documented (Wissinger 1997). However, this cross-habitat spillover movement may not actually be consistently or dynamically occurring, even during favorable conditions such as the peak growing season, due to the insects perceiving the edges as barriers. A recent review upholds this idea, finding that natural pest control services and pollination within an agricultural field decline exponentially with distance from border crop plantings, thus leaving the interior of fields with little to no pest control (Albrecht et al 2020). This suggests that cross-habitat spillover is limited, despite insect mobility, and therefore the landscape complexity created by the border crop has little impact on natural pest control, especially within the interior of an agricultural field. Better understanding border crops, their edges, and how insects interact in these environments will be extremely important for maximizing the ecological potential of this agricultural practice.

Insects acting as a natural pest control can play a huge role in reducing our reliance on agrochemicals, but more research needs to be done to understand insect movement, the fundamental agricultural system drivers, and their response to border crops. Even with the current research, there are still many unknowns. Currently, most research focuses on edge

dynamics at forest edges (Murcia 1995; Ries and Sisk 2004). However, the dynamics of forest edges will greatly differ from the dynamics of border crops and agricultural edges (Murcia 1995). Another gap in research is that the existing agricultural studies focus on only a few specific types of species, including lady beetles, aphids, and ground beetles (Rusch et al 2016). However, different insects can respond to the same edge in different ways, such as pests versus beneficials (Landis 2017; Ries and Sisk 2004), specialists versus generalists (Rand et al 2006; Ries et al 2004), and walking versus flying (Gardiner et al 2010; Schneider et al 2016). These make border crop edge effects highly variable. Further, most research that observes pest or beneficial communities focuses solely on the communities close to the edge. However, it is important to observe the communities at both the interiors and the bordering habitat types together (Rand et al 2006; Rusch et al 2016). A complete picture can give insight into how community patterns change between interior fields and natural habitats. In designing my research, I aimed to focus on these gaps in knowledge. I implemented a variety of agricultural border types, evaluated varying pest and beneficial insect communities, and studied the communities between habitat edges and interiors. The complexity of edge ecosystems makes it essential to have a comprehensive viewpoint, especially if we want to provide management implications for growers, farmers, landowners, and policy makers (Matson et al 1997; Rusch et al 2016).

While it is important to understand the broad complexity of the varying habitats and communities at an edge, it is also important to study edges through a narrower lens and to understand the mechanism of insect movement. While insects are mobile creatures, and thus it has often been assumed that cross-habitat spillover occurs, one of the main concerns surrounding agricultural edges is that insects may be perceiving edges as a barrier (Ries et al 2004; Mader et

al 1990). Research is needed to establish whether edges are indeed barriers, or in other words, if insects are crossing them or not (Tscharntke et al 2012; Rand et al 2006). Currently, most edge studies are observational and only provide abundance or richness data that lacks ability to evaluate direct movement patterns (Murcia 1995; Ries et al 2004; Ries and Sisk 2004; Rand et al 2006). More work must focus on navigation and tracking, especially for insects (Joo et al 2022; Nathan 2008). These studies must also be done across various and specific insect groups because responses can differ greatly (Tscharntke et al 2012; Joo et al 2022; Gardiner et al 2010). Further, most edge research focuses on movement from one habitat to another, but not in the reverse direction (Schneider et al 2016; Madeira & Pons 2016). In designing my research, I again aimed to focus on these limitations. I evaluated and compared actual movement sequences within different habitats and across different edge types by tracking marked beetles. Ultimately, this narrow mechanistic viewpoint establishes an important link to any observed overall pest and beneficial community patterns within agricultural fields and across their borders, and allows researchers and growers to justify decisions (Nathan 2008). This connection is crucial for making the border cropping practice more reliable and for more successful implementation in the future.

1.2 THESIS AIMS

Therefore, my master's project works to compare insect dynamics along habitat interior and edges, and to understand movement patterns between agricultural fields and adjacent habitat types. It also aims to gain insight into the effectiveness of border crops as a natural pest control. We conducted two scientific investigations to address these overarching goals: (1) an observational biodiversity field study and (2) an experimental mark, release, and recapture study. The observational biodiversity field study works to characterize and compare pest and beneficial insect communities across soybean fields that border either grass or corn habitats, and to

compare insect communities within habitat interiors and edges. This abundance, richness, and composition data provides the comprehensive viewpoint on insect dynamics needed to make bigger picture border crop and agrochemical management decisions more confidently. The experimental mark, release, and recapture study works to track movement patterns of ground beetles across soybean fields that border either grass or corn habitats. This study provides the intricate mechanistic details needed to determine the cross-habitat spillover movement sequences and to understand whether edges are barriers for insect movement. This two-part approach disassembles the complex relationship of insects at edges in agricultural landscapes to help improve natural pest control services. Ultimately, the two studies will help growers and scientists make predictions about pest pressure, navigate decisions about agrochemical use, and will alleviate border crops fears.

1.3 STUDY SYSTEMS

Addressing my questions within a soybean system provides interesting and important insights into agricultural management because it is a dominant and economically crucial crop in Kansas, and the entire Midwest region. It is used for food, animal feed, oil, and industry, and continues to expand in cultivation today (Garibaldi et al 2021). A soybean focus is also interesting because our results can extend to other beneficial insects that utilize border crops. For example, previous work shows that soybean productivity will increase with insect pollinators, even though soybean is a self-pollinating plant (Garibaldi et al 2021). Additionally, a review found that weed seed suppression will improve with invertebrate activity (Sarabi 2019).

Ground beetles (Coleoptera: Carabidae) are an ecologically important family within agricultural systems because of their ability to provide natural weed and pest suppression. Ground beetle adult and larval stages will opportunistically eat a diversity of weed seeds and pest

insects, including aphids, slugs, caterpillars, and other beetle larvae (Bohan et al 2011; Kulkarni et al 2017; Lövei and Sunderland 1996; Kromp 1999; Lindroth 1961; Erwin et al 1979).

Evidence of their weed and pest predation is documented across various species (Kulkarni et al 2017; Kromp 1999). In a laboratory experiment, Hance (1987) found that increasing ground beetle abundances were able to significantly reduce aphid populations. However, a ground beetle's contribution to natural pest suppression is largely dependent on environmental context and the surrounding landscape, including border crops. Many ground beetles require permanent natural habitat with suitable moisture levels, shade, soil type, vegetation cover, and food availability for survival, overwintering, and oviposition (Wallin and Ekblom 1988; Wallin 1985; Lövei and Sunderland 1996). Often, agricultural field interiors do not provide these necessary conditions, especially as harvesting, tilling, plowing, mowing, and grazing management practices create dangerous seasonal disruptions (Magura et al 2017; Landis et al 2000). Thus, to be effective natural pest suppressors, ground beetles must be able to shift between nearby natural habitat and agricultural field centers. However, a meta-analysis on edge response found that ground beetles reacted differently to various edge factors and reacted especially negatively to anthropogenic edges (Magura et al 2017). It is likely that the edge of a border crop and agricultural crop could inhibit cross-over between habitats. In this way, ground beetles are an interesting and important study organism for understanding edge effects, spillover movement, and they can provide interesting foundational implications for our border crop landscape dynamics study.

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Chapter 2 - Pest and beneficial insect abundance, richness, diversity, and community composition differ among habitats and along edges

2.1 INTRODUCTION

The increasing demand for agricultural crop production has led to large spans of single crop types and the reduction of crop variety and native habitats (Meehan et al 2011; Gámez-Virués et al 2015). This agricultural intensification has led to highly simplified landscapes that are depleted of natural resources, biotic contributors, and ecosystem services, including insect pollination and natural pest control (Spangler et al 2020; Dirzo et al 2014; Grab et al 2018; Tscharncke et al 2005). Without beneficial insects and the natural pest control services that they provide, pest pressure increases, agrochemical dependence increases, the quality of our food drops, crop productivity suffers, and disease becomes more common and can even spread more rapidly (Meehan et al 2011; Dirzo et al 2014; Grab et al 2018; Gámez-Virués et al 2015; Garibaldi et al 2021).

Incorporating diverse land cover types between large spans of annual crops can counteract these trends (Wagner et al 2021; Wagner 2020; Forister et al 2019; Dirzo et al 2014). Perennial grassland natural habitats strategically planted adjacent to agricultural fields can provide refuge, additional food, and shelter resources necessary for many beneficial insects' survival (Schulte et al 2017; Hopwood et al 2016; Redlich et al 2018; Landis et al 2000). The resulting increase in beneficial insect abundances has been linked to lower pest pressure (Landis et al 2000; Bianchi et al 2006; Rand et al 2006), which suggests that increased landscape complexity has the potential to create natural pest control services within agricultural fields. On the other hand, agricultural fields planted adjacent to other agricultural fields do not offer these same benefits. A study found that there were higher pest insect densities in landscapes with

higher proportions of agricultural fields (Grab et al 2018). This contrast shows that pest and beneficial insect communities within agricultural fields will likely depend on adjacent habitat types.

However, what affects the insect community structure within an agricultural field will likely be more complex than simply what habitat neighbors the field. Although a complex landscape, such as a grassland habitat neighboring a soybean field, should increase beneficial insects and decrease pests, this trend is not always observed. Some studies show that increased landscape complexity has little effect on pest abundance (Chaplin-Kramer et al 2011; Cox et al 2014), while other studies show it can even result in higher pest abundances (Fiedler and Landis 2007). Additionally, in a recent review, Albrecht et al (2020) found that natural pest control services decline exponentially with distance from perennial habitat plantings, thus leaving the interior of fields with little to no pest control. These results suggest that spillover of beneficial insects from natural habitats into agricultural fields is limited to the edges of the fields. An edge effect, where insects perceive the edge between neighboring fields as a barrier, may be occurring. The extent to which insect communities differ between edge and interior habitats needs to be studied.

Understanding the complexity of insect communities within an agricultural field then goes even further than analyzing the impact of crop habitat neighbors and field location on insect communities. Comparisons between different beneficial and pest insect groups must also be studied more closely because these groups can respond to the same agricultural edge in different ways (Landis 2017; Ries and Sisk 2004; Rand et al 2006; Ries et al 2004; Gardiner et al 2010; Schneider et al 2015). Beneficial insects could be attracted to a perennial grassland habitat within an agricultural cropping landscape, while pest insects are not. That circumstance would suggest

there is great potential for pest management. Alternatively, both beneficial and pest insects could be attracted to a grassland. This circumstance may lead to no significant net decrease in pest populations, and therefore less benefits from having the grassland nearby. However, many studies examining the role of landscape complexity on pest control focus on one or a few specific insect species at a time (Rusch et al 2016). To understand the overall impact of landscape complexity on pest suppression, examining both beneficial insects and pest insects at the same time needs to be considered (Rusch et al 2016; Martin et al 2013; Bianchi et al 2006).

The objectives of this study are to characterize both pests and beneficial insect communities across field edges and interiors to determine whether landscape complexity attracts insect groups differently. Furthermore, by observing and characterizing communities at both the edges and the interior of fields, changes in community structure might then give us insight into whether spillover into the adjacent habitat is occurring. For example, if there are no similarities of community structure between a neighboring grassland and an agricultural field, then movement between the habitats is likely not occurring. In contrast, if the community structure of beneficial insects is similar between neighboring grassland habitats and in the agricultural fields, then free movement of beneficial insects is possibly occurring between habitats. Therefore, our objective was to use pitfall and yellow sticky trapping techniques to characterize the overall pest and beneficial insect abundance, richness, and entire community compositions between agricultural fields and adjacent habitat types. Specifically, we ask (1) does community structure differ within different habitat types, (2) does community structure vary along edges compared to habitat interior, and (3) do these findings depend on the adjacent habitat type?

We predicted that beneficial and pest insects would vary among habitat types and along edge types. More specifically, assuming an edge effect would not be a barrier to movement, we

anticipated that beneficial insect abundance and richness would be highest within neighboring grassland habitats (Bianchi et al 2006) and near those grassland edges (Nguyen and Nansen 2018), and that they would decline within the agricultural field interior (Albrecht et al 2020). We hypothesized a reverse trend for the pest insect abundance and richness, due to predation. We predicted that these findings would be reflected by highly overlapping community compositions, with the edges being made up of an intermediate that widely encompassed the characteristics of its two adjacent habitats (Ries et al 2004; Fonseca 2008). Results from this research will provide a better understanding of how neighboring habitat landscape complexity can impact insects, including a variety of species at multiple locations within an agricultural field. The results will then have implications for the common practice of border cropping, or the planting of natural perennial habitat strips within or next to agricultural fields. Therefore, our research can inform growers and landowners about the benefits of landscape complexity to increase area-wide adoption of the practice.

2.2 MATERIALS AND METHODS

Study Area and Collection Design

To assess the impact of habitat and edge type on beneficial and pest insect communities, we conducted a two-year biodiversity study across twenty field sites within an agriculturally dominant region located in the surrounding Manhattan, Kansas area (39.1836°N, 96.5717°W) (Figure 1). Ten of the sites were paired fields of soybean that had an adjacent grassland habitat (soybean-grass), while the other ten sites were paired fields of soybean that had an adjacent corn habitat (soybean-corn). Half of these sites were surveyed in 2021 while the other half were surveyed in 2022. This experimental design enabled us to observe two different edge types, an agricultural-natural (soybean-grass) and an agricultural-agricultural (soybean-corn). We selected

soybean as our focal crop because it is a dominant and economically crucial crop in Kansas, and the entire Midwest region. It is used for human food, animal feed, oil, and industry, and continues to expand in cultivation (Garibaldi et al 2021). Additionally, pesticide active ingredients are commonly used in soybean fields. A national survey found that of the total planted acres, 98% were sprayed with herbicides and 20% with insecticides (NASS 2021).

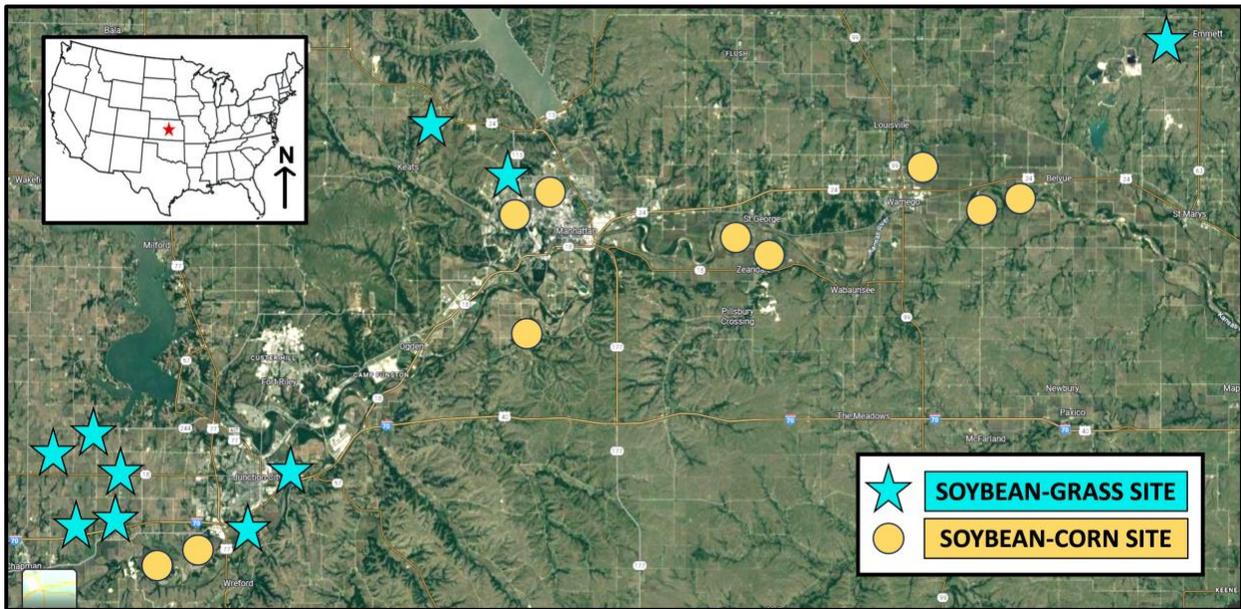


Figure 1. A satellite image of the soybean-grassland (n=10; solid blue star symbol) and soybean-corn (n=10; solid yellow circle symbol) established site locations near Manhattan, Kansas.

Within each site, we placed three transects; (1) within the interior of each soybean field, (2) within the interior of the bordering habitat (either corn or grass), and (3) perpendicular across the shared edge of the two habitats (Figure 2). Interior habitat transects were at least 20-meters away from all its field boundaries (Fonseca 2008).

Each transect consisted of five pitfall traps set approximately 10-meters apart and three yellow sticky traps set approximately 20-meters apart along a 40-meter line (Figure 2). Every

edge transect had four additional pitfall traps placed at one-meter and four-meter distances in both directions from the center trap and two additional sticky traps placed at ten-meter distances in both directions from the center trap (Figure 2). Pitfall traps were constructed from a 16-oz plastic cup, filled with 300-mL of non-toxic antifreeze preservative (diluted at a 1:1 ratio with water), placed into the ground so that it was flushed with the ground surface (Larsen and Work 2003). The trap was then secured into the ground with a grid of mesh overlay (0.5-inch opening; 12-in x 12-in square) and 6-inch garden stakes. The mesh overlay also prevented any bycatch of invertebrates or small vertebrates (Woodcock 2005). A cover, constructed from recyclable dinner plates and 12-inch landscape staples, was used to protect every pitfall trap from rain and disturbance by other animals. Sticky traps were composed of yellow cardboard slathered with un-baited adhesive and were attached to a thin steel core garden pole using extra-strength twist ties at the height of its location's vegetation. This trapping method enabled us to survey a more complete insect community because we gathered data from both ground dwelling and aerial insects.

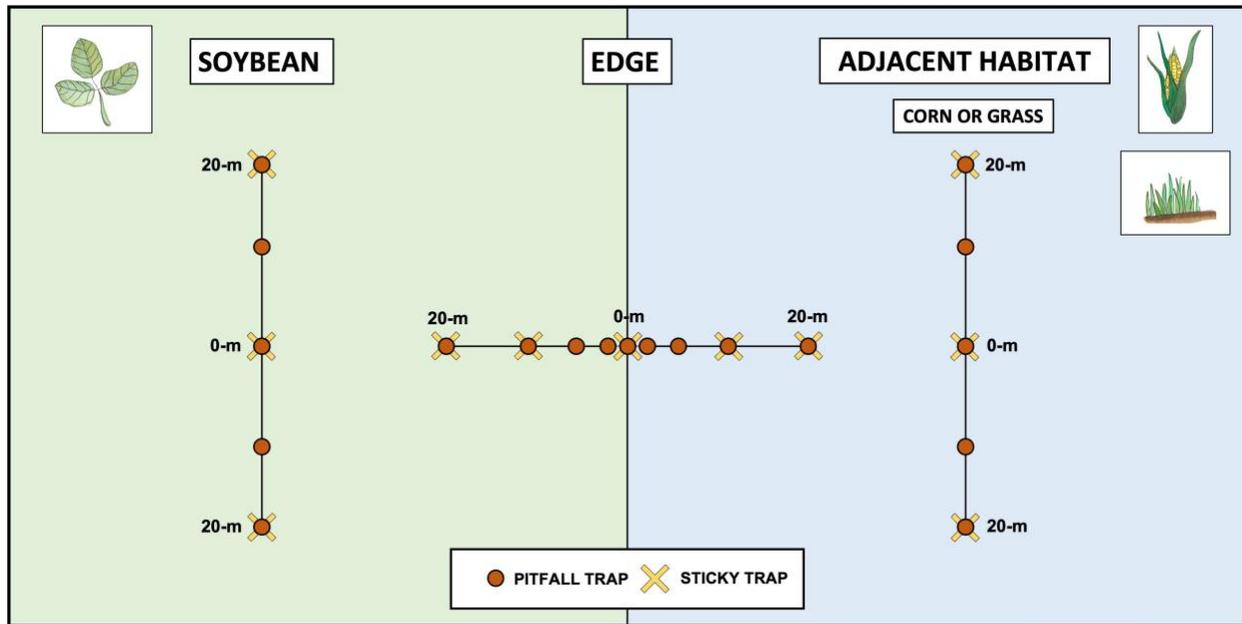


Figure 2. A descriptive image of the transect arrangement and placement (orange circles= pitfall trap; yellow X= sticky trap) within each established field site location.

Across the two-year span, a total of 60 transects containing 1,140 pitfall traps and 660 sticky traps, were deployed. Trapping transects remained in the field for six, one-week intervals during peak soybean growing season (three survey period in 2021 and three survey periods in 2022). However, in the first year of the study, the pitfall trap transects remained in the field for only 48-hours instead of the one-week interval in 2022. Therefore, insect captures were standardized by trap days in the field. Pitfall samples were washed and stored in 90% ethanol. Sticky samples were preserved with a thin film covering and stored at -20°C . All insects were sorted, identified to family. We assigned each family as “predators” and “herbivores” based on Kansas State University Extension Resources and the Kansas Department of Agriculture’s Insects in Kansas Book (Table 1).

Table 1. List of beneficial predators and pest herbivores caught in 2021 and 2022.

Order	Family	Common Name	Classification	% of Classification
Hymenoptera	Aphidiidae, Ichneumonidae	Wasps, Parasitic Wasps, Bees	Beneficial	34
Hymenoptera	Formicidae	Ant	Beneficial	24
Araneae	Araneae	Spider	Beneficial	14
Coleoptera	Staphylinidae	Rove Beetle	Beneficial	13
Coleoptera	Carabidae	Ground Beetle	Beneficial	7
Psocodea	Psocidae	Barklice	Beneficial	2
Coleoptera	Cantharidae	Soldier Beetle	Beneficial	2
Neuroptera	Chrysopidae	Green Lacewing	Beneficial	1
Coleoptera	Silphidae	Carion Beetles	Beneficial	<1
Coleoptera	Coccinellidae	Lady Beetles	Beneficial	<1
Coleoptera	Lampyridae	Firefly	Beneficial	<1
Coleoptera	Cincindelidae	Tiger Beetle	Beneficial	<1
Coleoptera	Lycidae	Netwinged Beetles	Beneficial	<1
Coleoptera	Mordellidae	Tumbling Flower Beetles	Beneficial	<1
Diptera	Tipulidae	Crane Fly	Beneficial	<1
Diptera	Syrphidae	Flower Fly	Beneficial	<1
Diptera	Tachinidae	Tachinid	Beneficial	<1
Diptera	Bombyliidae	Bee Fly	Beneficial	<1
Ephemeroptera	Ephemeridae, Baetidae, Caenidae, Heptageniidae	Mayfly	Beneficial	<1
Hymenoptera	Apinae	Bumble Bee	Beneficial	<1
Hymenoptera	Halictidae	Sweat Beet	Beneficial	<1
Hymenoptera	Braconidae	Parasitoid Wasp	Beneficial	<1
Neuroptera	Hemerobiidae	Brown Lacewing	Beneficial	<1
Odonata	Calopterygidae, Lestidae, Coenagrionidae	Dragonfly, Damselfly	Beneficial	<1
Plecoptera	Perlidae	Stonefly	Beneficial	<1
Trichoptera	Trichoptera	Caddisfly	Beneficial	<1
Orthoptera	Gryllidae	Cricket	Neutral	50
Coleoptera	Nitidulidae, Cucujidae, Erotylidae, Languridae	Sap, Flat Bark, Pleasing Fungus, Lizard Beetles	Neutral	49
Blattodea	Blattellidae	Cockroach	Neutral	<1
Coleoptera	Bostrichidae	Branch and Limb Borers	Neutral	<1
Hemiptera	Berytidae	Stilt Bug	Neutral	<1
Hemiptera	Cicadidae	Cicada	Neutral	<1
Hymenoptera	Mutillidae	Velvet Ant	Neutral	<1
Thysanoptera	Thripidae, Phlaeothripidae	Thrip	Pest	42
Diptera	Sciaridae, Cecidomyiidae, Culicidae, Simuliidae, Chironomidae, Dolichopodidae, Muscidae	Flies, Mosquitoes, Gnats, Gall Midges, Black Flies, Longlegged	Pest	31
Hemiptera	Aleyrodidae	White Fly	Pest	14
Hemiptera	Aphididae	Aphid	Pest	5
Hemiptera	Acanaloniidae, Flatidae, Dictyopharidae	Planthoppers	Pest	3
Coleoptera	Elateridae	Click Beetle	Pest	1
Isopoda	Isopoda	Pill Bug or Roly Poly	Pest	1
Hemiptera	Miridae	Plant Bug	Pest	1
Coleoptera	Scarabaeidae	Japanese Beetle	Pest	<1
Coleoptera	Curculionidae	Weevil	Pest	<1
Coleoptera	Scarabaeidae	Green June Beetle	Pest	<1
Coleoptera	Cerambycidae	Longhorned Beetles	Pest	<1
Coleoptera	Chrysomelidae	Leaf Beetles	Pest	<1
Coleoptera	Meloidae	Blister Beetles	Pest	<1
Coleoptera	Scarabaeidae	June/May Beetle	Pest	<1
Coleoptera	Tenebrionidae	Darkling Beetles	Pest	<1
Diptera	Tephritidae	Fruit Flies	Pest	<1
Hemiptera	Pentatomidae	Stink Bug	Pest	<1
Hemiptera	Psyllidae	Jumping Plant Lice	Pest	<1
Hemiptera	Lygaeidae	Seed Bugs	Pest	<1
Hemiptera	Tingidae	Lace Bug	Pest	<1
Hemiptera	Cercopidae, Cicadellidae, Membracidae	Froghoppers, Leafhoppers, Treehoppers	Pest	<1
Lepidoptera	Various Families	Butterflies, Moths	Pest	<1
Orthoptera	Tetrigidae, Acrididae, Tettigoniidae	Grasshopper	Pest	<1

Statistical Analysis

Pest herbivore and beneficial predator abundance, richness, and diversity (Shannon's H) were determined for each of the six transect locations: corn (interior), adjacent soybean (interior), corn-soybean edge, grass (interior), adjacent soybean (interior), and grass-soybean edge. Abundance was standardized to the number of insects captured per trap per day to account for differences in pitfall sampling periods between the two years and for trap disturbances caused by wildlife such as raccoons. Insect abundance and richness were totaled across the transects for each year and met statistical assumptions through a log-transformation ($\log_{10}(x+1)$).

To measure the effect of transect location type, we conducted separate two-way ANOVAs for both the total pest and the total beneficial predator insect abundances, richness, and diversity (six ANOVAs in total). Location type (corn-edge-soybean; grass-edge-soybean) and year (2021; 2022) were our predictor variables, while the abundances, richness, and diversity were our responses. Site was not included as a random effect in this model, as preliminary analysis showed it was not influential. Pre-determined Tukey HSD (honest significant difference) post-hoc multiple comparison of means tests was used to test the significance between transect location types.

To measure the effect of transect location type and year on the separate pest and beneficial predator insect community compositions, we conducted permutational multivariate analyses of variance (PERMANOVA; vegan R package: `adonis2`) based on a Bray-Curtis distance matrices (Warton et al 2012; Jackson et al 1989). Pre-determined Tukey HSD post-hoc multiple comparison of means tests was used to test the significance between location types. More specifically, for the interactive-argument PERMANOVA model, habitat type (corn-edge-soybean; grass-edge-soybean) was considered as the fixed grouping effect, while site was a

random effect. The multivariate insect community dataset (Log + 1 Transformed; Bray-Curtis) was the response variable. A principal coordinates analysis (PCoA) for each location type (corn-edge-soybean; grass-edge-soybean) was used to visualize these PERMANOVA findings. All analyses were completed in R v4.3.0 (R Development Core Team, 2023).

2.3 RESULTS

We collected 57 insect family groups, including 26 beneficial and 24 pest families, within the interiors and across the edges of working soybean fields that bordered either corn fields or grass natural habitats. There were significantly higher pest insect abundances within soybean field interiors compared to all other transect locations (Figure 3A: $F=41.9663$; $df=5,48$; $p<0.001$). The pest insects collected from those soybean interiors ($n=165,329$) accounted for 46.40% of our total pest sample, over five times more than within the grass interior ($n=28,878$) and over seventeen times more than the corn interior ($n=9,195$). Thus, location within the habitat was important because there were significantly higher pest insect abundances with the soybean field interiors compared to edges. However, bordering habitat type was not important because there were high pest abundances within soybean fields no matter the grassland or corn borders. There was also significantly higher pest insect family richness within soybean interiors compared to neighboring habitat types (Figure 3B: $F=9.2216$; $df=5,48$; $p<0.001$). However, unlike the abundance findings, pest insect family richness was significantly higher at the edges too. That pest richness edge effect was also somewhat present for the pest diversity findings. There was slightly higher pest diversity at the edges compared to each of the habitat interiors (Figure 3C), although this effect was not statistically distinguishable at the transect location level ($F=1.0901$; $df=5,48$; $p=0.378007$). Pest insect abundance ($F=24.1592$; $df=1,48$; $p<0.001$), richness ($F=50.4896$; $df=1,48$; $p<0.001$), and diversity ($F=8.1811$; $df=1,48$; $p=0.006249$) all responded

significantly to sampling years. There was higher abundance, richness, and diversity in the second year of sampling. Nevertheless, the same location patterns were upheld across both sampling years.

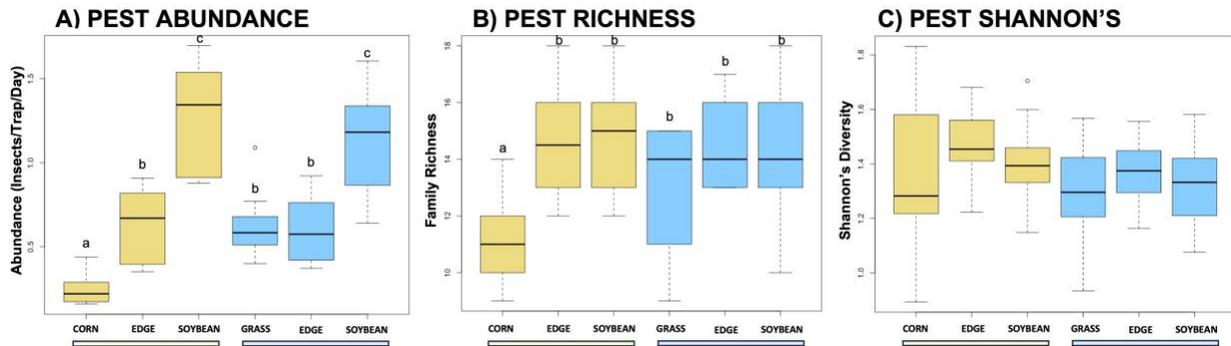


Figure 3. Boxplots reveal significant differences between transect location (corn-edge-soybean; grass-edge-soybean) and pest insect (A) abundance (insects/trap/day; log+1) and (B) richness, but not (C) Shannon's diversity.

Beneficial insect abundance (Figure 4A: $F=6.8221$; $df=5,48$; $p<0.001$) and richness (Figure 4B: $F=7.3490$; $df=5,48$; $p<0.001$), but not diversity (Figure 4C: $F=0.7745$; $df=5,48$; $p=0.5729$), was significantly impacted by habitat type and location. There were significantly higher beneficial insect abundances within the grassland interiors compared to the other habitat types. Thus, neighboring habitat type was impactful. Additionally, the neighboring habitat was also marginally important for soybean field interiors because the soybean fields bordered by these grasslands had slightly higher, although not statistically significant, beneficial insect abundances in comparison to the soybean fields that were bordered by the corn (Figure 4A). Despite the grassland abundance dominance, beneficial insect family richness was significantly higher at the edges. That beneficial richness edge effect was also somewhat present for the beneficial diversity findings. There was slightly higher diversity at the edges compared to each of the habitat interiors, although this effect was not statistically distinguishable at the transect

location level (Figure 4C). Only richness responded significantly to the second year of sampling ($F=14.7224$; $df=1,48$; $p=0.0003636$), yet the same location patterns were still upheld between years.

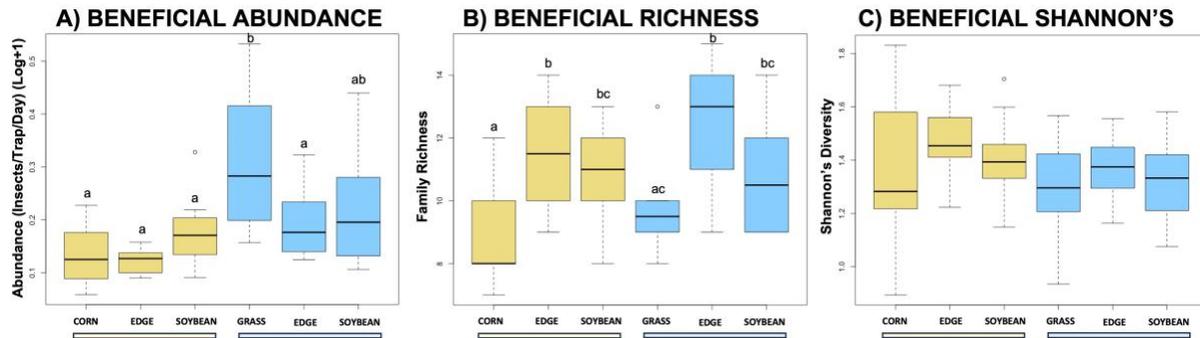


Figure 4. Boxplots reveal significant differences between transect location (corn-edge-soybean; grass-edge-soybean) and beneficial insect (A) abundance (insects/trap/day; log+1) and (B) richness, but not (C) Shannon's diversity.

The pest community at both the corn-edge-soybean and grass-edge-soybean sites varied significantly between habitats. For pest insects within the corn-edge-soybean sites, community composition significantly varied among transect types (Table 2A&B: $F=31.279$; $df=2,14$; $p=0.003$; $F=17.753$; $df=2,14$; $p=0.001$). Similarly, for pest insects within the grass-edge-soybean sites, community composition also significantly varied among transect type (Table 2C&D: $F=6.7507$; $df=2,14$; $p=0.003$; $F=3.1456$; $df=2,14$, $p=0.008$).

Table 2. Permutational multivariate analysis of variance of pest insect community compositions (Log+1 transformed; Bray-Curtis) revealed significant variations between habitat types. This suggests that pest insect communities are changing between habitats and across time. This was consistent between (A) corn-edge-soybean paired sites in 2021, (B) corn-edge-soybean paired sites in 2022, (C) grass-edge-soybean paired sites in 2021, and (D) grass-edge-soybean paired sites in 2022. The * indicates a significant p-value ($p < 0.05$).**

		Df	SumOfSqs	R2	F	Pr(>F)	
A)	HABITAT	2	1.5441	0.83905	31.279	0.003	**
	Residual	12	0.2962	0.16095			
	Total	14	1.8403	1			
B)	HABITAT	2	1.58743	0.74743	17.756	0.001	***
	Residual	12	0.53641	0.25257			
	Total	14	2.12384	1			
C)	HABITAT	2	0.56533	0.52944	6.7507	0.003	**
	Residual	12	0.50246	0.47056			
	Total	14	1.0678	1			
D)	HABITAT	2	0.27866	0.34395	3.1456	0.008	**
	Residual	12	0.53152	0.65605			
	Total	14	0.81018	1			

Principal coordinate analysis (PCoA) visually revealed that the pest edge community was significantly different and appeared to be an intermediate of the two adjacent habitats' pest identities when corn was the border (Figure 5A&B). This finding was consistent between years. PCoA also revealed that, when grassland was the bordering habitat, the edge community was similar to the grassland interior and the soybean interior was significantly different (Figure 5C&D). This finding was also consistent between years. Across both site types and years, the soybean and edge communities were driven and dominated by a variety of pest insect taxa (brown lacewings, green lacewings, aphids, thrips, hemipterans) while the corn and grass were mostly barren in their pest taxonomic drivers.

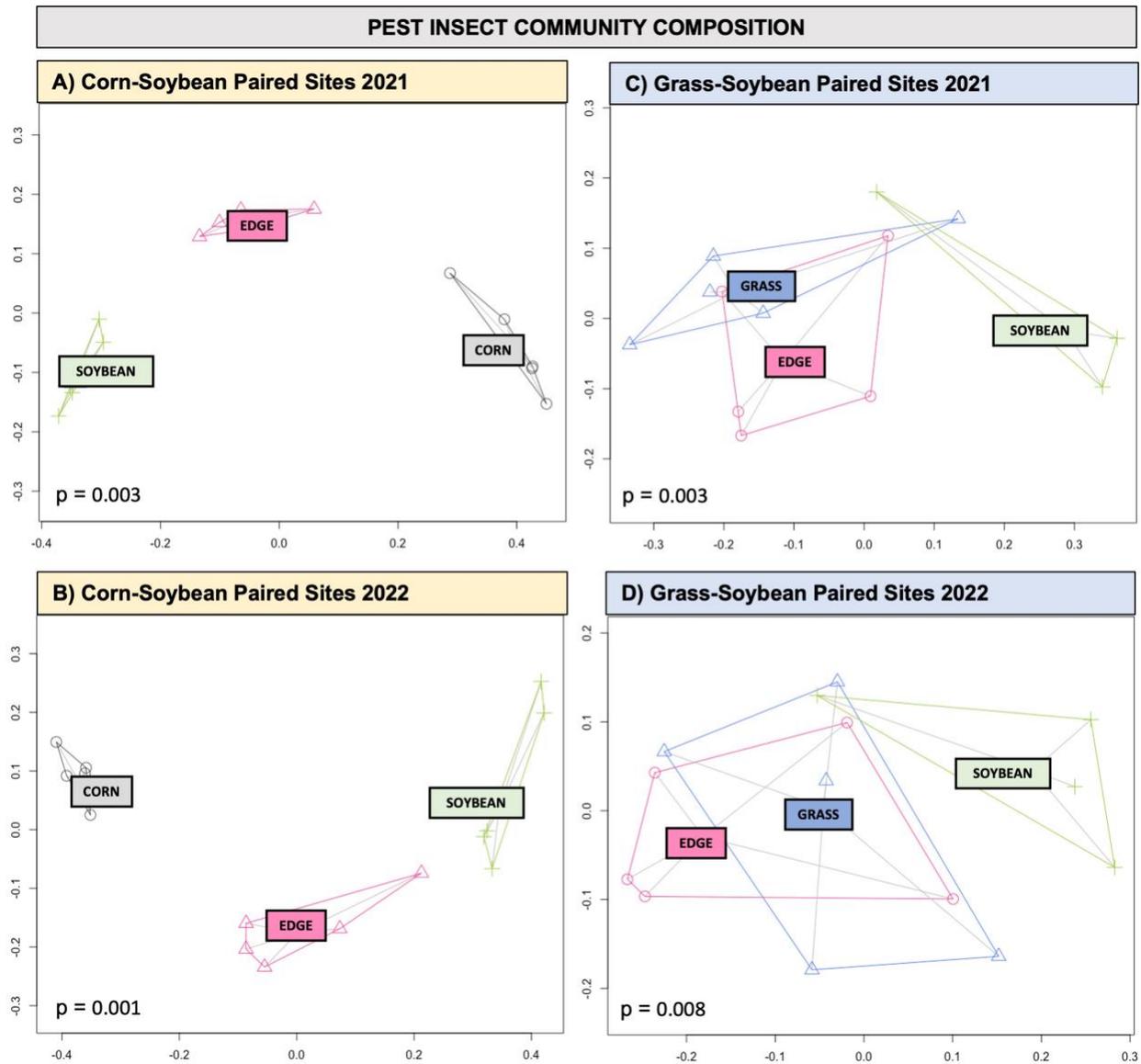


Figure 5. Principal coordinate analysis (PCoA) of pest insects reveals significant differences between different habitat types and the transformed (Log+1; Bray-Curtis) pest insect community matrix data for (A) corn-edge-soybean paired sites in 2021, (B) corn-edge-soybean paired sites in 2022, (C) grass-edge-soybean paired sites in 2021, and (D) grass-edge-soybean paired sites in 2022. For the corn-edge-soybean sites in 2021, the first PCoA axis explained 75.75% of the variation while the second explained 12.58% (A). In 2022, the first PCoA axis explained 67.91% of the variation while the second explained 14.86% (B). For the grass-edge-soybean sites in 2021, the first PCoA axis explained 71.31% of the variation while the second explained 13.82% (C). In 2022, the first PCoA axis explained 62.31% of the variation while the second explained 19.21% (D).

Like the pest community, the beneficial community at both the corn-edge-soybean and grass-edge-soybean sites varied significantly between habitats. For beneficial insects within the corn-edge-soybean sites, community composition significantly varied among transect types (Table 3A&B: $F=2.901$; $df=2,14$; $p=0.001$; $F=1.1625$; $df=2,14$; $p=0.004$). For beneficial insects within the grass-edge-soybean sites, community composition also significantly varied among transect types (Table 3C&D: $F=1.9761$; $df=2,14$; $p=0.002$; $F=1.9919$; $df=2,14$, $p=0.009$).

Table 3. Permutational multivariate analysis of variance of beneficial insect community compositions (Log+1 transformed; Bray-Curtis) revealed significant variations between habitat types. This suggests that beneficial insect communities are changing between habitats and across time. This was consistent between (A) corn-edge-soybean paired sites in 2021, (B) corn-edge-soybean paired sites in 2022, (C) grass-edge-soybean paired sites in 2021, and (D) grass-edge-soybean paired sites in 2022. The * indicates a significant p-value ($p < 0.05$).**

		Df	SumOfSqs	R2	F	Pr(>F)	
A)	HABITAT	2	0.4114	0.32663	2.9104	0.001	***
	Residual	12	0.84813	0.67337			
	Total	14	1.25954	1			
B)	HABITAT	2	0.16639	0.16231	1.1625	0.004	**
	Residual	12	0.85876	0.83769			
	Total	14	1.02516	1			
C)	HABITAT	2	0.41311	0.24775	1.9761	0.002	**
	Residual	12	1.25431	0.75225			
	Total	14	1.66742	1			
D)	HABITAT	2	0.38387	0.24924	1.9919	0.009	**
	Residual	12	1.15628	0.75076			
	Total	14	1.54015	1			

However, unlike the pest community, that beneficial community response differed between habitat types and between sampling years too. When corn was the bordering habitat in 2021, PCoA visually revealed that the edge community was significantly different from the two

adjacent habitats' identities (Figure 6A). There was a balance of beneficial taxonomic drivers within the soybean and the edge (parasitic wasps, mayflies, lacewings) while the corn was barren. However, when corn was the bordering habitat in 2022, the edge community became an intermediate of the two adjacent habitats' identities (Figure 6B). There was now a more even distribution of beneficial insect taxa (rove beetles, lacewings, spiders, mayflies) between all three habitats, including the corn. When grass was the bordering habitat in 2021, the edge community was an intermediate of the two adjacent habitats' identities (Figure 6C). There was an even distribution of beneficial insect taxa (ants, ground beetles, ladybeetles, lacewings, tiger beetles). However, when grass was the bordering habitat in 2022, the edge was similar to the soybean interior and the grassland interior was significantly different (Figure 6D). There was now a culmination of specific beneficial insect taxa within the soybean and the edge (lady beetles, ground beetles, bees, rove beetles) compared to the grassland (ants).

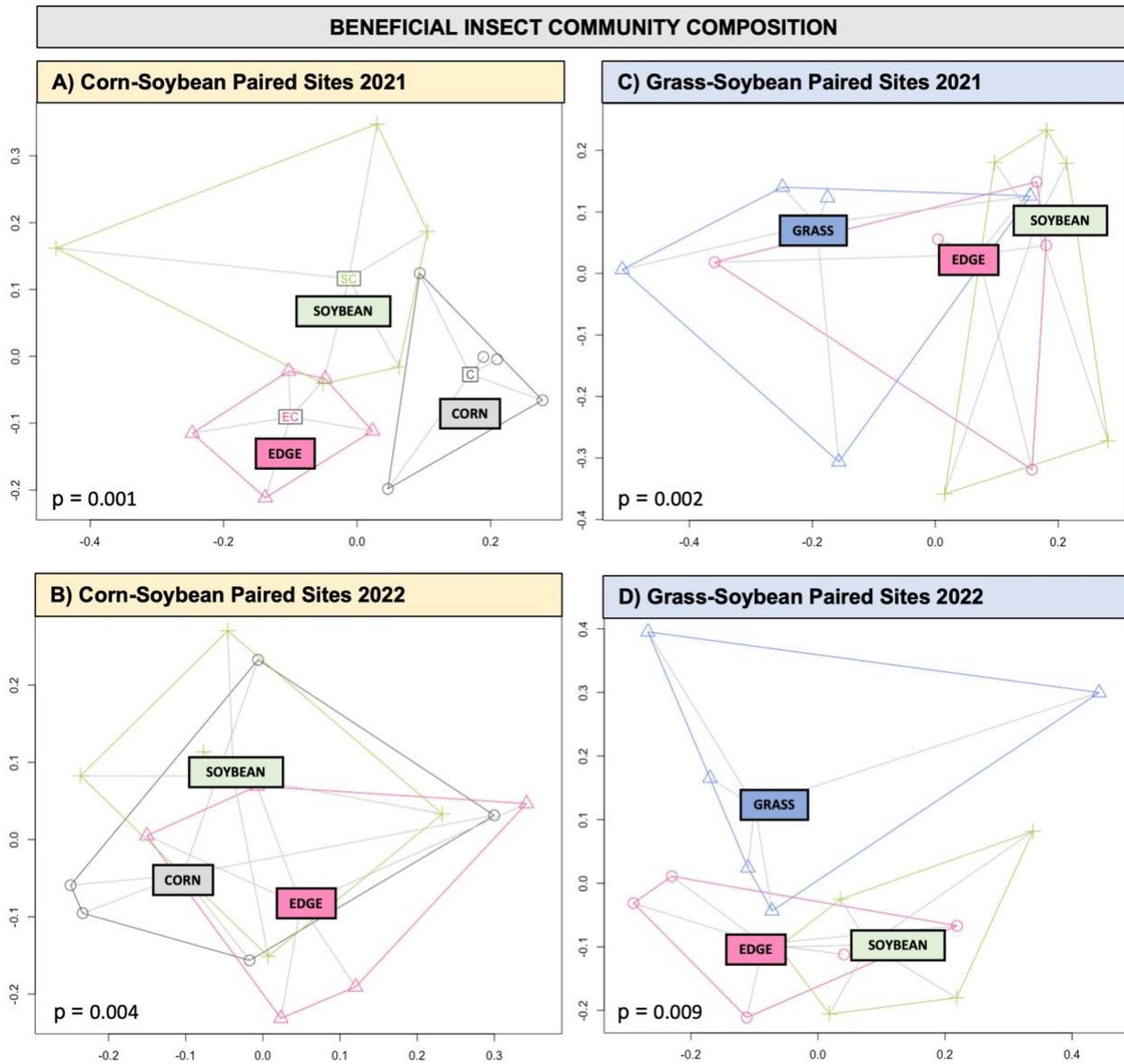


Figure 6. Principal coordinate analysis (PCoA) of beneficial insects reveals significant differences between different habitat types and the transformed (Log+1; Bray-Curtis) beneficial insect community matrix data for (A) corn-edge-soybean paired sites in 2021, (B) corn-edge-soybean paired sites in 2022, (C) grass-edge-soybean paired sites in 2021, and (D) grass-edge-soybean paired sites in 2022. For the corn-edge-soybean sites in 2021, the first PCoA axis explained 38.39% of the variation while the second explained 24.98% (A). For the corn-edge-soybean sites in 2022, the first PCoA axis explained 46.79% of the variation while the second explained 29.85% (B). For the grass-edge-soybean sites in 2021, the first PCoA axis explained 46.82% of the variation while the second explained 35.70% (C). For the grass-edge-soybean sites in 2022, the first PCoA axis explained 44.19% of the variation while the second explained 27.94% (D).

2.4 DISCUSSION

Our characterization of insects between agricultural field interiors, edges, and across adjacent habitat types provides a better understanding of the impact of landscape complexity on different insect groups. We found that pest and beneficial insect abundance, richness, diversity, and community composition varied between different habitats and edges. We also revealed that the strength of these patterns largely depended on neighboring habitat type, field location, and sampling year. Overall, we believe that increasing landscape complexity with grassland habitats, despite barriers to movement and some community separation, can positively impact insects. This research is crucial for border crop practice viability and management decisions, especially regarding natural pest control.

To begin, the differences in pest insect abundance, richness, and diversity between transect locations suggests that an edge effect is occurring. There were significantly higher pest insect abundances in soybean interiors than neighboring habitats. The edge abundances were intermediates between the two, which shows that the edge is probably impacting the surrounding areas and could be acting as a gradient or filter. These findings were expected because edges are known to cause changes in species dynamics (Ries et al 2004; Ries & Sisk 2010). The edges also had significantly higher overall pest insect richness and slightly higher diversity than neighboring habitats, which shows that edges could potentially be an optimal habitat and that pest insects are benefitting from the edges. This edge effect result was also expected because an edge can provide a wider variety of conditions and available resources between the different habitat types (Tscharrntke et al 2012; Rand et al 2006). Interestingly, these edge findings were consistent no matter the neighboring corn or grass habitat type. Usually, edge effects are largely context dependent (Porensky & Young 2013), so the consistency in pest abundance, richness,

and diversity between both corn-soybean and grass-soybean paired sites shows that these factors may not be as dependent on neighboring habitats.

In regard to beneficial insects, the differences in abundance, richness, and diversity between transect locations also suggests that an edge effect is occurring. There were significantly higher beneficial abundances in the grassland interior compared to its own edge and compared to all other habitat types. This suggests that beneficial insects prefer grassland and that they do not like edges. In this way, edge effects are largely context dependent on neighboring habitat type. However, the beneficial insect edge effect likely extends beyond a natural-agricultural edge type created from grassland plantings. There were significantly higher beneficial insect richness and slightly higher beneficial insect diversity at the edges compared to the neighboring habitats for both corn-soybean and grass-soybean bordering sites. This shows that the edge likely always impacts beneficial insects. Therefore, we must look more closely at community composition to understand the full impact of neighboring habitat type on both pest and beneficial insects. Nevertheless, from these measurements alone, it is still evident that an edge effect is occurring for pests and beneficials.

Like the abundance, richness, and diversity findings, our pest community composition findings show that an edge effect is occurring. What the pest community composition findings were able to show even further is that the neighboring habitats significantly changed what the pest edge effects were. For the corn-soybean paired sites, the corn communities were significantly different and separated from the soybean communities, while the edge communities were a unique intermediate of both those neighboring habitats. This finding suggests that an agricultural-agricultural edge limits movement between both neighboring habitat interiors, specifically from corn into soybean and from soybean into corn. However, for the grass-soybean

paired sites, we found that the barrier to movement was mostly in the direction from soybean to grass while movement likely occurred from grass to soybean. The soybean community was significantly different and separated from both the grass and edge communities, while the edge community compositions consistently reflected the grassland itself. This suggests that grassland communities are spilling over the edge into the soybean field.

The consistency across both sampling years of the pest community for each border type results suggests that the neighboring grassland habitats do not attract more pests and do not facilitate more pest movement than a corn neighboring habitat. Any spillover from the grassland into the soybean is extremely limited because there were significantly lower pest abundances within the grassland and the edge. Additionally, it is likely that a neighboring grassland habitat could attract pest insects away from a soybean interior while a neighboring corn habitat would not be as effective. This was also reflected in our abundance findings, as soybean fields that had a neighboring grassland habitat had slightly, although not significantly, lower pest abundances compared to soybean field interiors that neighbored corn habitats.

Similar to our pest community composition findings, our beneficial community composition findings also show that an edge effect is occurring. However, unlike the pests, the beneficial community composition findings between edge types and years were highly variable. Both the neighboring habitat type and the sampling year significantly changed the edge effect. For the corn-soybean paired sites during the first year of sampling, the corn communities were significantly different and separated from both the edge and the soybean communities. This finding suggests that an agricultural-agricultural edge limits beneficial insect movement in both directions, specifically from corn into soybean and from soybean into corn. However, the second year of sampling suggests that movement between habitats was now possible because the edge

communities were a unique intermediate of both the corn and soybean neighboring habitats. For the grass-soybean paired sites during the first year of sampling, the grass communities were significantly different and separated from the soybean communities, while the edge communities were a unique intermediate of both those neighboring habitats. This finding suggests that a natural-agricultural edge limits movement into both neighboring habitat interiors, but that spillover into the edges from both the grass into soybean and from the soybean into grass is possible. However, the second year of sampling suggests that movement patterns change. The grassland communities were now significantly different and separated from both the edge and the soybean communities. In this way, there was a barrier to movement in the direction from grass to soybean while some movement likely occurred from soybean to the grassland edge. Unfortunately, although we have found that movement of beneficial insects can occur between habitats, there are still significant differences between years and between these interior community compositions, meaning this movement is likely not to the extent which is needed for natural pest control.

The differences between the unique pest and beneficial corn-soybean and grass-soybean edge communities, and their probable two-way and one-way movement barriers depending on the sampling year, are somewhat surprising. Previous research has shown that ground beetles have been found to respond more strongly and more negatively to unnaturally developed anthropogenic edges and they have reduced ability to easily move between habitats and across edges (Magura et al 2016). Also, there is a greater species response and community differentiation to edges that have highly contrasting habitats on either side (Duelli et al 1990). Corn and soybean are more similar to each other, especially in terms of annual cycles, than grass and soybean. However, the corn-soybean edge was largely able to prevent movement both ways,

while the grass-soybean edge usually only prevented movement in a single direction. Previous research also shows that habitat permeability can be negatively affected by differences in vegetation height or vegetation densities between adjacent habitat types (Ries et al 2004). Both grass and corn are both quite different in height throughout various points in the growing season compared to soybean. Therefore, it would be expected that each of their edges would create a similar pest and beneficial community response. However, edge responses were quite different between grass and corn, and pests and beneficials. It is possible that the edge between a corn-soybean adjacent habitat is a more abrupt transition for pests compared to beneficial insects and is thus a greater barrier to movement than a grass-soybean edge. These results can be seen as good news because a comparably softer grassland edge that permits movement of insects, especially beneficial ones, into neighboring soybean fields, would be helpful in the application and adoption of border cropping practices for natural pest suppression.

In conclusion, our study findings suggest that while an edge effect is occurring, there can be some opportunity for beneficial insect spillover from grassland interior into a soybean field for natural pest control services. Unfortunately, that spillover depends on year and is limited to the edges. However, the habitat neighboring a soybean field does have a great impact. A grassland habitat would provide more landscape complexity, support more beneficial insects, and thus would provide greater potential for natural pest control services. A grassland habitat would also create a consistent mediating response for pest insects, which is a steadiness that growers often work to achieve in their cropping systems. These findings have many implications for border cropping practices. Implementation of various techniques, such as softening edges or using lures, would certainly be needed to make a grassland edge of a border crop more permeable and consistent across years, and therefore could more readily promote cross habitat

movement of beneficial insects and ultimately positively impact natural pest suppression in the future. However, an unmanaged grassland and its edge could still provide the slight and subtle regulating or mediating service on pest pressure within soybean interiors, which is desperately needed to offset today's intensification of agricultural systems. In this way, we feel that this study shows that border cropping is a low-risk practice that provides just enough reward for it to be worth it.

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Chapter 3 - Ground beetle movement is impacted by edge habitats in agricultural landscapes

3.1 ABSTRACT

Border crops are known to increase beneficial insect biodiversity within agricultural fields by supplementing insects with food and nesting resources. However, the effectiveness of border crops relies on insect movement between adjacent habitats and some insects might consider habitat boundaries as barriers. Therefore, insect movement between habitats needs to be more closely studied to understand the effectiveness of border crops for ecosystem services such as pest control. Our objective was to compare ground beetle (Coleoptera: Carabidae) movement across soybean plots that were bordered by corn and grassland habitat to determine whether habitat boundaries were considered barriers of movement to predatory beetles. Using a grid of pitfall traps within these habitats, we conducted a mark, release, and recapture experiment to track and evaluate ground beetle movement patterns. Results showed that it is likely that any edge habitat, including agricultural-agricultural boundaries and natural-agricultural boundaries, are barriers to ground beetle movement and even create separate communities. We found that ground beetles stayed in the environment of their release and that movement between habitats, no matter the type of bordering habitat or type of edge, was uncommon. However, we also found positive indications for increased natural pest control within soybean. Ground beetles selected soybean habitat over the grass or corn when placed at an edge and had similar movement activity levels between the grassland and soybean habitats. Therefore, making habitat edges more permeable, especially using various techniques such as softening edges or lures, could promote cross habitat movement and ultimately contribute to natural pest control.

3.2 INTRODUCTION

Beneficial insects provide natural pest control services worth around \$4.5 billion USD annually (Dirzo et al 2014), but have experienced significant declines from agricultural intensification (Wagner 2020; Wagner et al 2021; Forister et al 2019; Dirzo et al 2014). A sustainable agricultural border cropping practice could help alleviate these dramatic declines in insects and their natural pest control services while decreasing pest pressure and reducing insecticide use (Meehan et al 2011; Rusch et al 2016; Grab et al 2018). Border crops, which are perennial natural habitats strategically planted adjacent to agricultural fields, provide the additional shelter and food resources needed for beneficial insect survival (Schulte et al 2017; Hopwood et al 2016; Redlich et al 2018; Landis et al 2000). Therefore, increased beneficial insect abundance and diversity can provide valuable natural pest control services when they move into the adjacent crop habitat.

To elevate the effectiveness of beneficial insects and their impact on reduced pest pressure and insecticide use, their spillover from the natural habitat into the agricultural field center must be consistent. However, while mobile generalist insects have the physical capability of crossing habitat boundaries and can feed on resources in both habitat types, experimental results on spillover movement are mixed or spatially limited. In a recent review, Albrecht et al (2020) found that natural pest control services and pollination decline exponentially with distance from border crop plantings, thus leaving the interior of fields with little to no pest control. These results suggest that spillover benefits are limited to the edges of the fields. Additionally, Murcia et al (1995) found shifts in insect abundance and diversity at habitat edges because of the sudden dramatic change in habitat types, suggesting that habitat edges may limit cross-habitat movement. Similarly, Frampton et al (1995) found that different habitat types can

limit movement of ground beetles. They found grassland habitats to be less penetrable than a crop habitat, which prevented movement between grasslands and crop fields. These studies point to the idea that many insects perceive border crop edges as a movement barrier.

To understand the possible benefits of border crops for pest control services in agricultural fields, more research on insect movement patterns is needed. Because insect movement can be influenced by many factors, including edge abruptness, microclimate, food availability, and anthropogenic influence (Magura et al 2016; Rand et al 2006; Mader et al 1990), predictions about insect movement patterns are unclear and complex. For example, movement can be influenced by the adjacent habitat type and its physical characteristics (Madeira et al 2016), the type of insect (Magura et al 2016; Wallin & Ekbom 1988), the season (Labruyere et al 2016; Knapp et al 2019), and between directional viewpoints, either moving into or out of a grassland border crop (Nathan et al 2008; Rand et al 2006; Schneider et al 2016). Tölgyesi et al (2018) found that mowed grassland habitats, which mimicked haying practices, impacted ground beetle assemblages, and reduced ground beetle spillover into neighboring habitats, compared to un-mowed grassland strips. Additionally, Knapp et al (2019) found that ground beetle distribution, abundance, and richness within agroecosystems varied between seasons and between different species. Unfortunately, the actual spillover patterns of insects are not well documented (Joo et al 2022; Nathan 2008). By tracking the actual movement patterns at the habitat edges, especially during peak growing season, it is possible to have a better understanding of the prevalence of spillover movement and therefore make better agricultural management decisions (Tschardt et al 2012; Thomine et al 2020).

Our research objective is to characterize cross-habitat movement between agricultural fields and adjacent habitat types using mark, release, and recapture techniques. We focused on

the habitat use and movement patterns of ground beetles (Coleoptera: Carabidae) as they are an ecologically important family within agricultural systems because of their ability to provide natural weed and pest suppression. Ground beetle adult and larval stages will opportunistically eat a diversity of weed seeds and pest insects, including aphids, slugs, caterpillars, and other beetle larvae (Bohan et al 2011; Kulkarni et al 2017; Lövei and Sunderland 1996; Kromp 1999; Lindroth 1961; Erwin et al 1979). This predation is documented across various species of ground beetles (Kulkarni et al 2017; Kromp 1999). In a laboratory experiment, Hance (1987) found that increasing ground beetle abundances were able to significantly reduce aphid populations, a major pest in agricultural fields. These beneficial qualities are a major reason the ground beetle was selected as the study organism.

Ground beetles are also ideal study organisms because their abundances, and thus their overall contribution to natural pest suppression, is largely dependent on environmental context and the surrounding landscape. Many ground beetles require permanent natural habitat with suitable moisture levels, shade, soil type, vegetation cover, and food availability for survival, overwintering, and oviposition (Wallin and Ekbohm 1988; Wallin 1985; Lövei and Sunderland 1996). Often, agricultural field interiors do not provide these necessary conditions, especially as harvesting, tilling, plowing, mowing, and grazing management practices create dangerous seasonal disruptions (Magura et al 2016; Landis et al 2000). Thus, to be effective natural pest suppressors, ground beetles must be able to shift between nearby natural habitat and agricultural field centers. However, a meta-analysis on edge response found that ground beetles responded differently to various edge factors such as its origin (natural or anthropogenic) and management practices (grazing, mowing, or burning) and most responses were negative to anthropogenic edges (Magura et al 2016). In addition, ground beetles' lower dispersal ability from walking

compared to flying aerial insects, and thus their smaller activity levels and home ranges, often make adjacent habitats largely influential on their community dynamics (Gardiner et al 2010). Therefore, the edge of a border crop and agricultural crop could inhibit cross-over between habitats.

For the mark, release, and recapture experiment, we specifically asked (1) do ground beetle movement patterns vary within different habitat types, (2) does movement vary along edges, and (3) is cross habitat movement frequent and if so, does it vary depending on habitat type and beetle groups? We predicted that movement patterns would vary among habitat types and along edge types. More specifically, we predicted it would be greatest and most dynamic within grassland interiors and around the grassland edge compared to other habitat and edge types. We also hypothesized that these effects would differ between ground beetle groups and individuals. We predicted that smaller ground beetles will be extremely limited and disproportionately impacted by edges. Results from this study will provide insight into the effectiveness of border crops for conservation practices and area-wide adoption of the practice.

3.3 MATERIALS AND METHODS

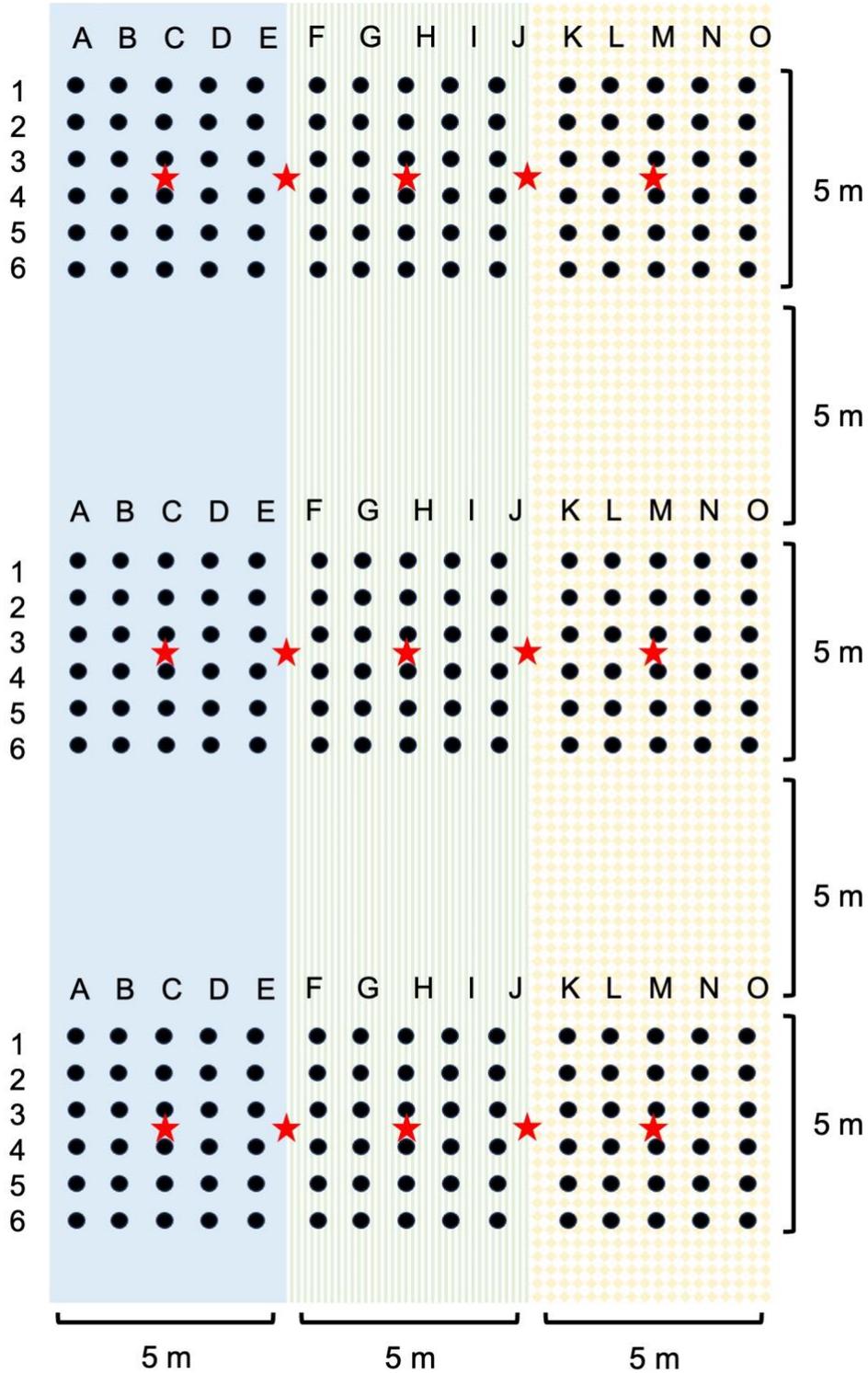
Study Area and Field Site

To monitor ground beetle movement between different habitat types and across edges, we conducted a mark, release, and recapture experiment at the Agronomy North Farm property of Kansas State University in Manhattan, Kansas (39.212817, -96.601856). The North Farm is a 15.7-acre agricultural center for education, research, and extension and situated at the northern end of the city. A strip of forested area, positioned towards the south of our plots, provided a wind break and separation from a nearby residential area.

For the mark, release, and recapture, we established neighboring strips of grassland, soybean, and corn where each habitat strip was 25-meters long and 5-meters wide (Figure 7). A square grid of thirty pitfall traps (5-m x 5-m in size), was placed into each habitat where each trap was one-meter apart. Therefore, a single spatial block contained 90 total traps across the span of its three habitats (5- x 15-meters). Each pitfall trap was constructed from a 16-oz plastic cup that was punctured with small basal pin holes to allow for water drainage and placed into the ground so that it was flushed with the ground surface (Larsen and Work 2003). A mesh overlay cover (0.5-in opening; 12-in x 12-in square), secured with garden stakes, was used to protect live beetles within each pitfall trap from predators.

There were three spatial blocks within the entire field, each block spaced five meters apart (Figure 7). We did not fence the spatial blocks, thus allowing beetles to freely move from block to block. The consecutive and continuous positioning of pitfalls, habitats, plots, and blocks were purposeful as it allowed for ground beetles to be captured across a wider range of distances, both within and across plots. It also allowed us to observe two different border types, a natural-agricultural (grass-soybean) and agricultural-agricultural (soybean-corn) to determine whether border types included the likelihood of movement.

Figure 7. Mark, release, and recapture experimental field site set up. Black circles represent pitfall traps, each spaced one meter apart. Red stars indicate beetle release points. The blue solid column represents grassland habitat, the green striped column represents soybean habitat, while the yellow spotted column represents corn habitat.



Mark, Release, Recapture Setup

To obtain ground beetles for the movement tracking, we collected specimens from beetle communities from our already established field site. These initial ground beetle captures (hereafter referred to as “original captures”) were brought to the lab, identified to tribe, and a unique number and color was drawn onto the elytra using nontoxic, low odor, and quick dry TFIVE Oil-based Paint Markers. Paint markers were chosen for their efficiency and effectiveness for marking insect exoskeletons. We tested this technique in a preliminary greenhouse experiment before transition to the field, and it has also been effectively used in previous ground beetle movement studies (Frampton et al 1995). Most of the original captures came from the grass (n=191; 62%), which suggests habitat preference, suitability, and higher abundances for the grassland natural habitat. The grass abundance was over twice the abundance from either the soybean (n=81; 26%) or corn (n=40; 13%) habitats.

The marked original capture ground beetles were returned to the field site and re-distributed evenly at five release points within each plot: (1) grass interior, (2) grass-soybean edge, (3) soybean interior, (4) soybean-corn edge, (5) corn interior (Figure 7). Beetles released within habitat interiors were placed directly at the center (2.5-meters into the 5-meter square). Beetles released at the edge were placed directly where the two habitats met. Thus, we released beetles from fifteen different points across the study field.

We monitored the traps daily for three weeks, which was to the point where no marked beetles were being recaptured. For each marked beetle recapture event, the date, habitat type, plot number, pitfall location, unique ID, and tribe were recorded. Then, the marked individual was re-released adjacent to the pitfall trap it was caught in, ultimately making it viable again for another capture. We released 317 total beetles representing eight tribes across two sampling

sessions in July and August 2022. Marked beetles included 115 Harpalini, 91 Pterostichini, 64 Megacephalini, 31 Scaritini, 6 Carabini, 4 Chlaeniini, 4 Brachinini, 1 Pasimachini, 1 Cicindelini.

Statistical Analysis

We calculated distance travelled per day for each captured ground beetle based on release and recapture location. We constructed a dispersal kernel to determine the distribution of movement distance for each recaptured beetle. Because of the spatial locations of the habitats, soybean (Figure 7; middle column) had a greater likelihood of recaptures than the neighboring grassland and corn columns, therefore we standardized the number of recaptures based on the likelihood of recaptures using the dispersal kernel. We compared standardized recapture location and distance travelled using analysis of variance and predetermined Tukey post-hoc multiple comparison of means. Chi-square contingency tests were used to assess the distributions and compare frequencies between ground beetles released and recaptured in different habitat locations.

3.4 RESULTS

A total of 70 marked ground beetles representing six tribes were recaptured 120 times for a 37.85% recapture rate. Of the recaptured tribes, Megacephalini was recaptured the most (n=28) and at the highest rate (43.75%), while Brachinini was the fewest (n=1) and Pterostichini was the lowest rate (15.38%). Three of the released tribes, Pasimachini, Chlaeniini, and Cicindelini, were not recovered. These were the least common tribes from the original captures, as only six individuals across the three tribes were released.

Overall, the majority of the beetles did not travel far distances and remained close to their release point (Figure 8). The median travel distance was 4.62 meters. Slightly over half the ground beetles (n=31; 51.43% of recaptures) moved between a total of 0.5-5.0 meters. The mean

travel distance was 9.25 meters. Several beetles (n=10; 14.29% of recaptures) moved over 20 meters, with the maximum being 48.78 meters. Further, these standout long travel distances came from the Megacephalini and Harpalini beetle tribes. However, the average movement patterns were consistent between tribes, despite apparent variability in body size, as none moved significantly more or less when compared to each other (Figure 9: $F_{5,64}=1.133$, $p=0.352$).

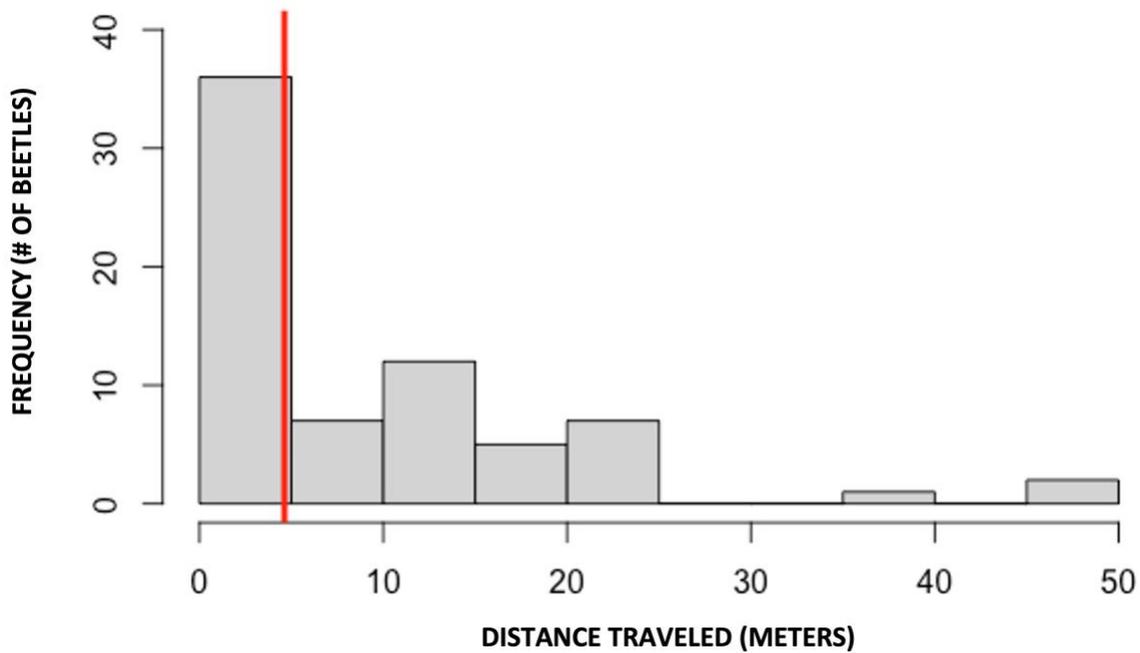


Figure 8. Histogram of ground beetle total distance traveled from release point. The red line signifies the median distance (4.62 meters).

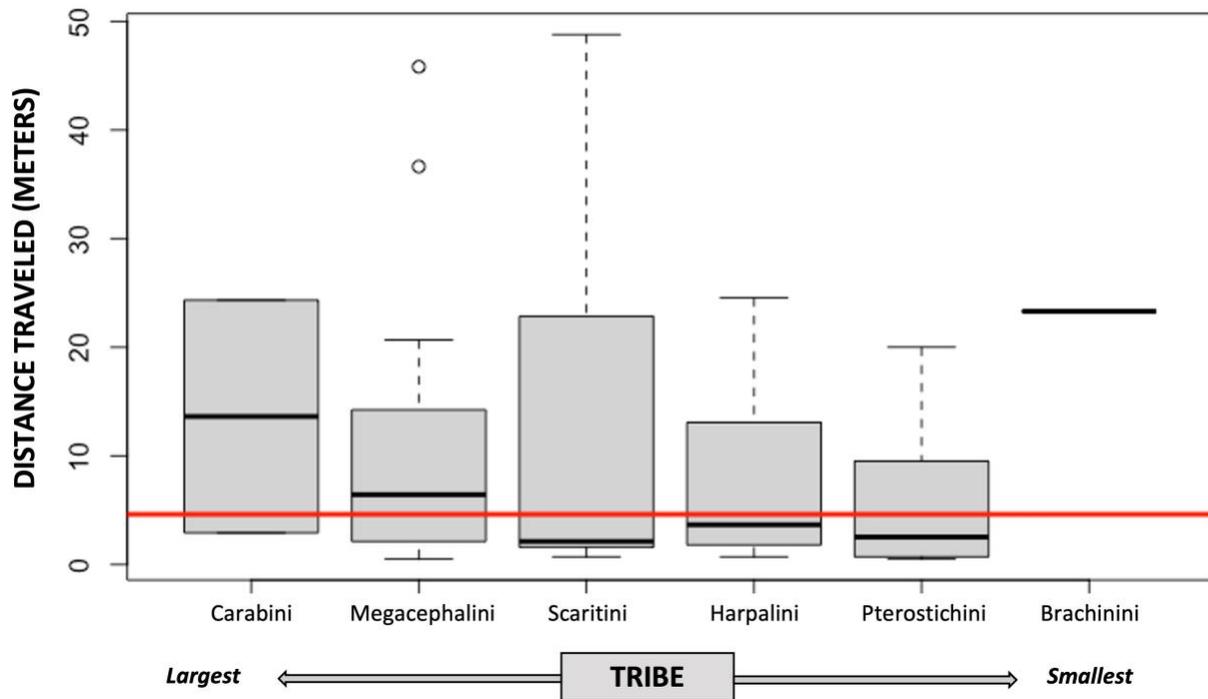


Figure 9. Boxplot shows there was no effect of beetle tribe on distance traveled ($F_{5,64}=1.133$, $p=0.3520$)

Evaluating travel based on release and recapture locations revealed that ground beetles largely remained within the same habitat that they were released in (Table 4; $X^2=38.57$, $df=4$, $p<0.001$, $n=83$). However, when beetles were released directly on the edge of two habitats and therefore forced to choose a habitat on either side, they selected the soybean at a higher rate than would be considered random (Table 5; $X^2=4.10$, $df=2$, $p=0.129$, $n=37$).

Table 4. Contingency table shows that ground beetles remained in the same environment they were released in ($X^2=38.57$, $df=4$, $p<0.001$, $n=83$).

		Release Habitat		
		Grass	Soybean	Corn
Recapture Habitat	Grass	66%	24%	0%
	Soybean	22%	65%	35%
	Corn	13%	12%	65%

Table 5. Contingency table shows that ground beetles selected soybean at a higher rate than expected when placed on the edge and forced to choose a habitat ($X^2=4.10$, $df=2$, $p=0.129$, $n=37$).

		Release Habitat	
		Edge	Edge
		Grass-Soybean	Soybean-Corn
Recapture Habitat	Grass	26%	11%
	Soybean	68%	61%
	Corn	5%	28%

Both these findings of remaining in the release habitat and choosing soybean at the edge, were consistent between tribes. However, the Harpalini tribe selected the soybean at a higher rate than the other tribes. All recapture records show that Harpalini always chose soybean when released at any edge (natural-agricultural and agricultural-agricultural). The results also show that, even when released in the center of either the grass or corn habitats, Harpalini found their way to the soybean and were frequently recaptured there. However, these movements into the soybean were not different from the median travel distances, as they only had to move a minimum of 2.5-meters to make it into the soybean habitat from the grass or the corn. No other

tribe findings suggested preference for any habitat when released in another habitat center, as most remained in that same habitat they were released in.

Recapture activity levels, as characterized by the percent of recaptures based on the probability of recapture in relation to their release location, were similar between the grass (19.0%) and soybean (18.6%) habitats, but lower in the corn (13.2%) habitat. Although there was less recapture activity in the corn, the ground beetles that were released in the corn center still traveled the same average distance as those released in the center of the grass habitat that had the highest activity levels (6.50 meters).

Movement events between habitats were uncommon. Only 12.5% of the total tracked movement patterns resulted in a travel across the grass-soybean edge (n=15) and 11.7% resulted in a soybean-corn edge crossing (n=14). There was no preference in the directionality across these natural-agricultural border crossings (n=7 events from grass to soybean, n=8 from soybean to grass). Similar patterns were found for the agricultural-agricultural border (n=7 events from soybean to corn, n=7 from corn to soybean). The edge crossing events came from less than a third of the total recaptured ground beetles and were dominated by three tribes, Megacephalini (n=11), Harpalini (n=8), and Pterostichini (n=5). All recaptured tribes documented at least one crossing event.

3.5 DISCUSSION

Our mark, release, recapture research with ground beetles works to provide better understanding of cross-habitat spillover of insects in human modified landscapes and delivers important insight on the effectiveness of border cropping practice for both grower management and ecosystem functioning. We found that ground beetles stayed in their release environment. We also revealed that despite an original preference for grassland, ground beetles selected

soybean habitat when placed at an edge and even had similar activity levels between the grassland and soybean habitats. These findings suggest that generalist ground beetles are adapted to survive in a variety of habitats which could be beneficial for biological control for numerous insects. However, we found that movement between habitats, no matter the type of bordering habitat or type of edge, was uncommon, suggesting that any edge habitat or sharp habitat boundaries, including border crops, are barriers to ground beetle movement. Therefore, for border crop practices to be successful for natural pest suppression, the implementation of various techniques, such as softening edges or using lures, are needed to facilitate and promote cross habitat movement of these generalist beetles.

The fact that ground beetles mainly moved short distances, no matter their location or habitat, suggests that there is community separation and that edges are barriers to movement between habitats. Wallin and Ekblom (1988) traced ground beetle species movement patterns with harmonic radar and found that, when a beetle is most active, it could move between two to six meters per hour in a cereal field. Several of our ground beetle individuals displayed the ability to perform these types of dynamic movements that cover longer distances (48.78 meters). However, the median total travel distance for all our beetles (4.62 meters) was much lower than these longer distance findings. It is possible that this short distance is due to the beetle's inability to cross edges, which were five meters apart in our experimental set up. This is especially relevant considering most of our ground beetles would only need to travel about half their median distance (2.5 meters) from their release point before running into an edge. While uncaptured beetles could have traveled farther distances than our experimental set up could assess, another possibility for the observed small-scale movement is that movement might not be

linear, as most ground beetles implement random search tactics and will turn frequently while searching for food or optimal conditions (Lövei and Sunderland 1996).

The fact that ground beetles remained close to their release point, no matter the location or habitat, suggests that the recaptured ground beetles are habitat generalists, meaning that they are likely to do well in any habitat. However, the grassland habitats still appear to be necessary for attracting and supporting ground beetle populations. It is well documented that natural habitats are higher in ground beetle diversity and species richness compared to crop habitats (Rischen et al 2021). Our study also produced findings that support this previous research because most of our original ground beetle captures came from the grassland and that the highest recapture activity level of all habitats occurred in the grassland too. Nevertheless, the ground beetles' continued presence within soybean and corn interiors could be a signal that they are benefitting from being there, especially because ground beetles are greatly opportunistic (Erwin et al 1979). Also, we found that when ground beetles were placed at habitat boundaries, they were later found in soybean, suggesting a preference for soybean. There were high recapture activity levels in the soybean too. It is possible that the soybean habitat contains different food sources compared to grassland. Ground beetles are known to eat a diversity of weed seeds and agricultural pest insects (Bohan et al 2011; Kulkarni et al 2017; Lövei and Sunderland 1996; Kromp 1999; Lindroth 1961; Erwin et al 1979). In this way, their hunger cues could drive ground beetles into and keep them within soybean. However, studies that investigated the impact of starvation on ground beetle travel into agricultural fields produced conflicting results (Frampton et al 1995; Wallin & Ekbohm 1988). It is possible that a food driven selection of soybean is present for ground beetles only during the peak growing season, and that grasslands provide an essential permanent and undisturbed nesting habitat during the rest of the year.

Another study found that beneficial insects, including ground beetles, use agricultural habitats when conditions are favorable, such as at peak growing season, which is when our study occurred, and that they retreat to natural areas when conditions are hostile, such as post crop-harvest (Wissinger 1997). Ground beetles are likely utilizing the soybean fields for their food potential, but still rely on grasslands for their needs.

Although ground beetles were found to utilize soybean fields and would benefit from movement between the grasslands and agricultural fields, the edges were found to be a barrier to movement. The limited crossings between both natural-agricultural to agricultural-agricultural borders show that both edge types are mostly impenetrable and suggest that habitat edges might be barriers to movement. This finding fits with previous studies that have also shown that many edge types, including dirt roads, paved roads, and grassy banks, all significantly reduce ground beetle population movement (Mader et al 1988; Duelli et al 1990; Frampton et al 1995).

However, this finding also slightly conflicts with previous studies that suggest an agricultural-agricultural edge could be much more permeable than a natural-agricultural edge. Allema et al (2019) found that ground beetles had greater mobility within agricultural fields and were less mobile within grass natural habitats due to ground cover being a movement barrier. Similarly, Duelli et al (1990) found that ground beetles crossed agricultural-agricultural field boundaries more often than other edge types, including natural-agricultural edges.

Further, the crossings that did occur in our studies only came from a few ground beetle tribes. Of the few edge crossings that we observed, most were dominated by three of the six total beetle tribes. A meta-analysis conducted on ground beetle community abundances and assemblages at natural and anthropogenic forest edges showed that edge response differed between species (Magura et al 2016). Our Megacephalini tribe accounted for around one third of

the total crossing events. These big-headed tiger beetles are large, nocturnal, flightless predators that rely on their eyesight to capture prey and are common around lake or river edges (Ball & Bosquet 2010). Their size, affinity for edges, and aggressive predator tendencies likely contribute to their agricultural edge crossing abilities. In contrast, we only recorded a single crossing event of the Brachinini tribe between the soybean and corn fields. This bombardier beetle's smaller size, in comparison to the big-headed tiger beetle, probably made crossing an edge more difficult. It has been reported that smaller beetles, those with less dispersal ability, are likely more affected by field boundaries (Frampton et al 1995).

Implications for the Border Cropping Practice

Overall, our findings show that ground beetles are habitat generalists and are active in all three habitat types. Additionally, the infrequent habitat crossings show that edges are barriers to movement. In this way, for the border cropping practice to have benefits for pest suppression, further management might be needed to promote cross-habitat movement. Specifically, the implementation of various techniques, such as softening edges or using lures, could make habitat edges more permeable and could promote cross habitat movement further infield. A softer, more gradual, and smooth transition between habitat types would facilitate travel. Magura et al (2016) found that highly managed anthropogenic edges were much more impenetrable in comparison to natural edges. Because our ground beetles displayed few edge crossings, this practice would have great potential to make an immense impact on movement and natural pest control. At the moment, our study shows that more research needs to be done for border crops to be used as large-scale agricultural pest suppression. This work is crucial, especially as agricultural intensification continues to drive insect biodiversity declines, deplete ecosystems, and the need to regain a more diverse and structurally complex landscape intensify.

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Chapter 4 - Conclusions

My master's project worked to provide a better understanding of insect dynamics and movement between agricultural fields and adjacent habitat types. It also delivered insight into the effectiveness of border crops as a natural pest control and conservation practice. We achieved these goals by conducting an observational biodiversity field study and an experimental mark, release, and recapture study. Overall, we found that any edge, including a grassland-agricultural edge like a border crop's edge, created separate communities and was a barrier to movement. Therefore, we concluded that increased habitat complexity created by grassland has little impact on natural pest control by ground beetles, especially within the interior of an agricultural field, but our results could inform future research and border crop practice modifications.

We found that an edge creates a separation between habitat types and is a barrier to movement from both a wider comprehensive viewpoint (the observational study) and a narrower mechanistic viewpoint (the mark, release, and recapture study). From our observational study, we found that entire pest insect communities were concentrated within soybean interiors while the beneficial insect communities largely remained within the grassland interiors. Further, both the pest and beneficial communities were significantly separated from their adjacent habitats. These findings alone provided strong evidence that an edge prevented movement. However, that conclusion became much stronger when linked to the mark, release, and recapture study that documented actual movement sequences within those same habitat and edge types. We found that individually tracked ground beetles rarely crossed edges. That scarcity became especially notable because our ground beetles remained in their corn or soybean release habitat despite their known preference for grassland and their known ability to move greater distances compared to the five meters of our experimental setup. Therefore, we could infer that our ground beetles,

along with pest and other beneficial insect species, commonly encountered edges but were unable to cross them.

Despite our finding above, we also found that some cross-habitat spillover occurred at a limited scale. From our observational study, we found that there were slightly more beneficial insects and slightly fewer pest insects within soybean fields that bordered grassland natural habitat compared to corn fields. This suggests that neighboring habitat types are important for insect community structure in soybean fields. A neighboring grassland habitat could support more beneficial insects that then successfully move into the soybean field interiors and eat pests. However, it is likely that this dynamic was driven by only a few specific beneficial insect groups that could actually cross the edge barrier. From the mark, release, and recapture study, the majority of our tracked edge crossings came from only two ground beetle tribes. In this way, spillover is possible but uncommon for most beetles, pest insects, and beneficial insects.

Our findings also suggest that a grassland-agricultural edge could be a similarly strong barrier to movement as an agricultural-agricultural edge. In our biodiversity study, the communities at the grassland-soybean edge were a strong reflection of the interior grassland communities, suggesting movement is possible from the grassland interior to the edge of the soybean, but not in the reverse direction. In contrast, the communities at the corn-soybean edge were distinct from the neighboring habitats, suggesting that cross-habitat movement was not occurring in either direction. The mark, release, and recapture experiment findings, however, did not support cross-habitat movement with any edge type, suggesting that the similarity in insect community structure in the grassland-soybean paired sites of our observational study could be due to the same generalist insect species residing in soybean and grassland. In this way, it is

reasonable to think that grassland-soybean edges, or other types of border crop edges, are still an especially strong barrier to movement and spillover.

Despite a hard grassland edge, there is potential for the border cropping practice for pest suppression by ground beetles. Our results showed that ground beetles selected soybean when placed on an edge and when given their choice of habitats, including the selection of soybean over grassland on a grassland-soybean edge. It is likely that ground beetles, and other beneficial insects too, if given the opportunity, are benefiting or could benefit from soybeans in some way, possibly as a food source. If management strategies are implemented to reduce edge effect and make smoother transitions between habitat types, then there would be greater opportunity for effective border cropping pest control. Strategically planting a gradient of intercropped grasses or soybeans across the edge and into the two bordering habitats could possibly soften the edge, minimize abruptness, and reduce the perception of a grassland edge as a barrier by insects. As a result, there could be more continuous movement between grassland and soybean, which could ultimately result in greater pest predation.

Of course, more work on insect dynamics and movement between agricultural fields and adjacent habitat types must be conducted to make the border cropping practice, and even our new management idea, more viable. Future work should continue to investigate the culminating pest and beneficial community dynamics and the ground beetle movement patterns at various scales. This work is crucial, especially as the perpetual cycle of increased agricultural intensification, greater pest pressure, and increased insecticide use accelerates our ecosystems into even more dangerous states.

Overall, our project successfully provides a greater understanding of border crops and edges in agricultural landscapes. The abundance, richness, and community composition data

provided the comprehensive viewpoint on insect dynamics needed for big picture functioning. The experimental mark, release, and recapture study provided the intricate mechanistic details needed to determine cross-habitat spillover movement sequences and to better understand edges as barriers. These two perspectives are essential for strategically increasing landscape complexity, better border cropping, and improved agrochemical management decisions and for scientific and ecological improvements. This project was also needed to bridge the gaps between the currently disconnected broad and narrow scopes and between scientific lenses. In conclusion, we were able to successfully disassemble the complex relationship of insects at edges within agricultural landscapes.