

EFFECT OF CONSERVATION-ORIENTED MANAGEMENT ON CARABID
(COLEOPTERA: CARABIDAE) COMMUNITIES IN AGRICULTURAL LANDSCAPES

By

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ABSTRACT

Agricultural landscapes in the last century have expanded to meet the global demands of food, fuel, and fiber necessary to support growing populations. Although the innovation of equipment, technology, and intensified agricultural practices have contributed to world food production, it has come at the cost of habitat loss through pollution or fragmentation, and a decline in global biodiversity, in particular, the decline of insect populations. Highly simplified agricultural landscapes have low habitat diversity, habitat amount, and simplified configuration that limits the dispersal of insects and their provision of ecosystem services that sustain crop yield via pollination, pest suppression, and nutrient-rich soils. As agriculture is a primary global land use, the threat of insect loss amid the uncertainty of changing climates will have lasting effects on global food security for generations to come. As such, it is necessary to shift from intensive systems dependent on high-input of pesticides, tillage, or monocultures, to agricultural landscapes that are multifunctional and support both human and ecosystem health and resiliency.

Perennial prairie strips or prairie plantings are a conservation tool to enhance ecosystem service provision in simplified landscapes and provide alternative habitat and food resources for wildlife. Insects contribute to agriculture through necessary ecosystem services and may benefit from the establishment of non-crop prairie plantings in agroecosystems. This dissertation focused on ground beetles, or carabids (Coleoptera: Carabidae) as beneficial predators of insect pests and weed seeds. Carabids are useful indicators for ground-dwelling arthropod diversity as they are sensitive to changes in agricultural management both above- and belowground, and benefit from the addition of native non-crop habitat within agricultural landscapes. In 2019, prairie strips were planted in two conservation-oriented treatments at the Kellogg Biological Station (KBS) Long-term Ecological Research (LTER) Main Cropping Systems Experiment (MSCE) in southwest Michigan. The two treatments include Reduced Input, using one-third the conventional application of pesticides, and Biologically Based, using no synthetic inputs. In this dissertation, I investigated **a)** the effects of long-term management and cropping treatment, before the addition of prairie strips, on carabid diversity and activity-density; **b)** how establishment of perennial prairie strips influenced carabid community composition in both the strip and adjacent row crop; and **c)** the spillover of predation services from the prairie strip into the row crop.

In Chapter One, I broadly reviewed the literature on agricultural landscape simplification and agricultural intensification, including the current global biodiversity crisis. I further

described historic and current conservation interventions to reduce biodiversity loss and augment ecosystem services within agriculture. The majority of the literature review focused on carabids as beneficial providers of pest and weed seed management, and the impact of various agricultural practices on the diversity and abundance of carabids within agroecosystems. In [Chapter Two](#), I addressed questions raised in the literature review of the long-term impacts of agricultural management on carabids by comparing the 2019 carabid community at the KBS-LTER to a similar study conducted in 1994-95. I found a severe decline in carabid abundance and a turnover in carabid species from the previously dominant community. Although we did not determine a singular reason for the decline, innovation in pest and weed management over the last three decades, including the widespread application of pesticides, likely reduced prey abundance and compounded the effects of landscape simplification on resource availability. In [Chapter Three](#) I investigated the effects of prairie strip establishment on carabid community composition, including the spillover effects from the prairie strip into the adjacent row crop. Carabid activity-density doubled one year after seeding the prairie strip, and the response to prairie strips varied by cropping treatment. I also found that after four years, prairie strips contributed to increased biodiversity both within the strip and within the center of the row crop. Given the evidence for spillover of carabid community biodiversity from prairie strips, I further studied the potential for pest suppression services in [Chapter Four](#). Using sentinel insect pests commonly found in Midwest, US agriculture and exclosures to limit predation to arthropods, I found relatively high pest suppression across treatments and a preference for prairie strips during early- and late-season when resources are scarce in agricultural landscapes. I conclude my findings in [Chapter Five](#) and discuss the broader implications of my dissertation research on conservation interventions for the prevention of biodiversity loss and ecosystem service provision, including key limitations or challenges of current sampling methods or experimental designs, and opportunities for future research in this field. Agriculture is not a closed system and neither is scientific research; in [Appendix One](#) I describe my community-engaged research project on prairie strip adoption. By conducting focus groups and partnering with Conservation Districts, I review farmer perspectives on challenges to the future of agriculture, and best practices for prairie strip establishment and maintenance in Michigan. By supporting ecosystem health in agricultural landscapes, we can also support the health and productivity of farming communities.

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LIST OF ABBREVIATIONS

ANOVA/AOV	analysis of variance
CLE	Conservation Lands Experiment
GLMM	generalized linear mixed model
GLM	generalized linear model
KBS	W. K. Kellogg Biological Station
HaH	Habitat Amount Hypothesis
LTER	Long Term Ecological Research
MCSE	Main Cropping Systems Experiment
NMDS	non-metric multidimensional scaling
SsC	Sorenson's Similarity Coefficient
SDI	Shannon's Diversity Index
PERMANOVA	permutational multivariate analysis of variance

CHAPTER ONE: LITERATURE REVIEW ON GROUND BEETLE (COLEOPTERA: CARABIDAE) COMMUNITIES IN AGRICULTURAL LANDSCAPES

ABSTRACT

Intensified agricultural practices over the last century have contributed to pollution, habitat loss, and global biodiversity decline. However, conservation interventions that establish alternative habitat and resources for beneficial pollinators, natural predators, or soil-dwelling organisms improve not only ecosystem health, but crop yield. Perennial prairie strips or plantings are one such conservation tool used to enhance ecosystem services within agricultural landscapes and combat ongoing biodiversity loss. Ground beetles, or carabids (Coleoptera: Carabidae), provide beneficial pest and weed seed suppression in cropping systems and are useful bioindicators for ground-dwelling arthropods within agricultural landscapes. As they are active both above- and belowground, carabids are sensitive to changes in immediate and long-term agricultural management and landscape simplification. Conservation practices, such as perennial prairie strips, have the potential to increase carabid and beneficial arthropod abundance, diversity, and service provision in agricultural landscapes.

The following literature review examines the consequences of agricultural practices on natural biodiversity and ecosystem health, and how the community composition of carabids is influenced in agroecosystems, including landscape structure, the changing climate, and intensive management. This literature review serves to provide the foundational knowledge for my following dissertation chapters and identify gaps in the collective scientific knowledge on carabid communities and conservation within agriculture that will be addressed by my dissertation research.

LITERATURE REVIEW

Agricultural Intensification and Impacts on Landscape, Biodiversity, and Ecosystem Services

As the human population increases, so too does the demand for food production, innovation, and expansion of agricultural practices. The Green Revolution in the mid 20th century led to a focus on production of high yielding commodity crops throughout the world. In the following decades, advancements in pesticides and genetically-modified crops, as well as the political and environmental push for biofuels to replace non-renewable energy sources, has led to high input, monocultural landscapes. Global commodity crops, including

wheat (*Triticum spp*), corn (*Zea mays* L.), rice (*Oryza spp.*), cotton (*Gossypium spp*), and soybean (*Glycine max* L.), are a primary source of food and income for much of the world (Khoury et al. 2014), and Green Revolution practices have contributed to reduced hunger and poverty (Pingali 2012). Where Green Revolution practices have not been prevalent, consequences to human well-being and food security could arise. For example, agricultural advancement is needed in sub-Saharan Africa where the increase in farming households outpaces the availability of arable land; the subsequent rapid urban growth from the migration of poor, rural farms will lead to food insecurity without high-yielding crop varieties, pesticides, and advanced equipment (Jayne et al. 2010; Ricker-Gilbert et al. 2014).

While beneficial in many respects, agricultural intensification resulting from the Green Revolution has also led to environmental degradation and negative consequences for human health. For example, when rice was grown as a subsistence crop in the Philippines, farmers were also able to grow non-rice crops and fish from the rice paddies to meet their nutritional needs. The introduction of GR practices and high pesticide input has limited farmers' ability to grow non-commodity foods or harvest fish (Pingali 1955; Pingali 2012). In the United States, advancements from GR practices have led to the surplus of commodity crops, which has incentivized farmers to shift from labor-intensive systems of livestock and high-diversity feed crops to row crop monocultures (Jackson 2008). The following decades of federal policy subsidized crops like corn, wheat, and soybean while discouraging alternative crops. Moreover, the consolidation of commercial production further limits farmers to grow only what is profitable on the market (Jackson 2008). As a result, agricultural landscapes in the U.S., are dominated by intensively managed crop monocultures at the expense of more diverse, natural landscapes. In the Cornbelt of the Midwest, U.S., although most of the land is held by small landowners, large and intensively managed commercial farms are expected to continue to increase in size (Spangler et al. 2020).

Intensive practices occur both at local and landscape scales. Locally, these include increased farm acreage, high input of pesticides and fertilizers, soil cultivation and tillage; landscape intensification includes the fragmentation or conversion of natural landscapes to few, specific crops (Tscharntke et al. 2005). The reduction of diverse landscapes and their distribution across the landscape, combined with the ecological consequences of high-input agriculture have led to biodiversity loss and long-term damage to natural ecosystems.

Simplification of Landscape Composition and Configuration

The structure of agricultural landscapes is a critical component of biodiversity and the provision of ecosystem services globally. At present, agricultural landscapes comprise ~ 40% of global land uses (Sustainable Food and Agriculture 2020) and support ecosystem services essential to the economic, cultural, or physical health of humans (Daily 1997). Provisioning services from agriculture such as crop yield are maintained by supporting services such as decomposition and nitrogen fixation and regulating services such as pollination and pest suppression (Daily, 1997; Chee, 2004). Fahrig et al. (2011) describes “functional landscape heterogeneity” as a blueprint to support the provision of services valuable to agricultural production, concurrent with services that support biodiversity and ecosystem health. However, continued intensification and agricultural expansion poses a risk to maintaining the functional value of agricultural landscapes.

Historically, a typical Midwest US farm consisted of livestock, diverse feed and row crops, and a network of fencerows and fallow patches alongside natural landscape features such as woodlots, prairies, grasslands, and wetlands (Jackson 2008). This heterogeneity of the landscape contributes to biodiversity and supports ecosystem functioning, as ecosystems are more resilient to disturbance when there is a diverse species pool to maintain populations in patch or isolated habitats (Tscharntke et al. 2005; Tscharntke et al. 2007). This structuring of the landscape is broken down into compositional heterogeneity (the diversity of cover types within a landscape) and configurational heterogeneity (the pattern and distribution of cover types) (Fahrig and Nutton 2005; Fahrig et al. 2011). Simplification occurs at the level of individual farms and expands to entire landscapes when diverse cropping systems shift to intensively managed monocultures (Tscharntke et al. 2005; Landis 2017).

Impacts to Biodiversity and Ecosystem Services

Landscape configuration and composition are valuable concepts in understanding the impact of agricultural expansion on biodiversity and species richness, particularly for arthropods, mammals, and birds that provide ecosystem services, such as pollination or pest predation (Landis, 2017; Martin et al., 2019). In part, species richness can be attributed to the total habitat amount, regardless of the size and isolation of non-crop habitat patches (Fahrig 2013). As non-crop habitats provide both an avenue for dispersal and provision of food and nesting resources, they are invaluable in agroecosystems. Cropland expansion limits the diversity, frequency, and

distribution of non-crop habitats within agricultural landscapes and has resulted in the loss of global biodiversity and ecosystem services (Foley et al. 2005; Bianchi et al. 2012). Multiple studies have shown that landscape change has a greater impact than agronomic practices alone, and that increased crop monocultures within the landscape result in reduced diversity of natural predators (Rusch et al. 2016; Haan et al. 2020). In contrast, diversity of natural landscape features may safeguard natural biodiversity and provision of ecosystem services; fragmentation and isolation of these habitat patches due to agricultural intensification and expansion will make them susceptible to disturbance or human-mediated change and risk their beneficial services (Tscharntke et al. 2005).

Intensification in the US Midwest

The Midwestern, US is an agricultural region of 51 million ha spread across eight states (Michigan, Illinois, Indiana, Iowa, Minnesota, Missouri, Ohio, and Wisconsin), of which approximately 75% is dedicated to annual crop production (USDA Land Use 2022). Corn and soybean (*Zea mays* L. – *Glycine max* L.), and to a lesser extent wheat (*Triticum aestivum* L.) dominate the cropped landscape. Productivity in this region is dependent on intensive agricultural practices, including row crop monocultures and inputs of synthetic pesticides and fertilizers.

Biodiversity

The biodiversity of birds, mammals, and arthropods within agroecosystems have been impacted by the loss or fragmentation of habitat due to cropland expansion and landscape simplification. In Canada and the US, 74% of birds associated with farmlands and grasslands have experienced population declines as compared to birds in other habitats; further, insectivorous birds faced higher declines due to a reduction in flying insect populations (Hallmann et al. 2017; Stanton et al. 2018). Predatory mammals (foxes, raccoons, skunks, weasels, etc.) predominantly avoid agricultural landscapes, and the resulting fragmentation of their habitat from agricultural expansion and disturbance regimes has led to reduced prey availability; long-distance dispersal abilities and generalist diets are favored in these landscapes (Gehring and Swihart 2003).

The sudden decline in insect biodiversity and abundance is of particular concern. Recorded declines of insects started in the mid 20th century, and current global research places the loss at nearly 45% (Wagner et al. 2020) with a 75% decline in flying insects (Hallmann et al.

2017). Climate change, loss of natural land due to degradation and exploitation, the conversion of land for agriculture, and widespread use of agrochemicals are possible causes (Hallmann et al. 2017), and endemic specialist species are being replaced by habitat or diet generalists (Wagner et al. 2020). Insects have long played an important service-providing role within agriculture, contributing to the suppression of crop pests, pollination, and nutrient cycling. Landscape simplification and habitat loss or isolation of semi-natural lands in agroecosystems may also contribute to the decline of beneficial arthropods (Bianchi et al. 2006; Tscharntke et al. 2012; Rischen et al. 2021). Butterfly diversity is highest in diverse agricultural landscapes with combinations of grasslands, forests, and diverse crop, and lowest in landscapes dominated by row crop monocultures with little semi-natural land (Meehan et al. 2013). Pollinators, such as honey or wild bees, are vulnerable to habitat and resource loss within agroecosystems and require diverse foraging and nesting material; as wild bees can augment the current loss of honeybee hives and their associated pollination services, a decline in their populations could have serious consequences both economically and ecologically (Kremen et al. 2002).

Air and Water Quality

Agricultural production in the United States is driven by the demand for food, fiber – and especially – fuel; in the ongoing effort to move away from fossil fuels, the United States has doubled-down on their commitment to corn ethanol production. The Renewable Fuel Standard (RFS), passed under the Energy Policy Act of 2005 and later amended, increased the expectation for renewable fuel production from 4 billion gallons/year in 2006 to 36 billion gallons/year by 2022, which would require a 40% increase of current corn production levels in the US (Hoekman et al. 2022). Although renewable fuels are considered a step in the right direction, ethanol production requires mass amounts of land, water, and resources to meet RFS expectations despite only marginal improvements in greenhouse gas emissions from standard fossil fuels (Hill 2022; Lark et al. 2022). To meet demand, there is concern that growers may convert land previously in the Conservation Reserve Program (CRP) and convert it back to corn production (Secchi et al. 2009), which would further degrade available wildlife habitat and resources for beneficial arthropods. Although ethanol may burn “cleaner” than gasoline or diesel via reduced carbon dioxide (CO₂) emissions, indirect emissions from ethanol production contribute to increased global emissions and reduced air quality. A review by Hoekman et al. (2012) associates the indirect costs of energy-intensive corn production to agronomic practices such as

cultivation and application of soil amendments or irrigation, drying of the corn for storage, production of ethanol, and the transport of ethanol via trucks or rail. Without mitigation or conservation efforts, increased demand for row crops managed through traditional agriculture will continue to have detrimental impacts on air and water quality.

Eutrophication

Agricultural activity in the Midwest and the overuse of soil amendments for row crops has resulted in eutrophication of the local and regional watersheds. Increased nutrient runoff (phosphorus and nitrogen) from agricultural inputs, combined with warming temperatures, have led to increased events of harmful algal blooms dominated by potentially toxic cyanobacteria (Watson et al. 2016). Algal blooms are ecologically harmful, as they deplete available oxygen and nutrients available to aquatic organisms, ultimately altering the trophic cascade; blooms are also detrimental for economic reasons as Lake Erie is a popular tourist and recreational location (Watson et al., 2016). Regional agricultural runoff to the Mississippi watershed has also resulted in the eutrophication of the Gulf of Mexico (Turner and Rabalais 2004). Globally, the loss of soil and nutrients from agricultural runoff has depleted the biodiversity and health of coastal waters, including economic losses to local fisheries and coastal communities (Boesch and Brinsfield 2000). Implementing mitigation practices within row crop agriculture may decrease the occurrence of harmful algal blooms, despite warming conditions and increased rainfall. Techniques aimed at reducing agricultural runoff include limitation or careful timing of fertilizer applications, conservation cropping, restored wetlands, and in-and out-field vegetation strips to filter or catch runoff (Watson et al. 2016; Fraker et al. 2023).

Crop Yield

Large monocultures of continuous crop management are the prevailing standard of traditional agriculture to increase yield and efficiency of production. However, there is mounting evidence that crop diversity and rotation not only increase yield but result in positive ecological outcomes. In a meta-review of central US farming systems by Bowles et al. (2020), they found that crop rotation resulted in increased yield in 9 of 11 systems and increased with the diversity or complexity of crops used (i.e., cereals and legumes vs. two cereals). Further, they found that crop diversity also improved the resilience of the fields against stress factors, such as drought in corn.

A Call for Change

The ecological consequences of intensive agriculture are clear. Conservation strategies within agriculture have been shown to reduce the ecological consequences of intensive practices and offer an option for a more sustainable food system. Agricultural landscapes can be multifunctional (Bommarco et al. 2013; Landis 2017) supporting ecosystem and human health. For example, research shows that complex agricultural landscapes, consisting of forest, riparian, prairie, grassland, and crops better support wildlife habitat and enhance ecosystem services (Tscharntke et al. 2005; Tscharntke et al. 2012; Landis 2017). Multifunctional agroecosystems sustain crop yield through the integration of ecosystem services that support biodiversity conservation (Geertsema et al. 2016). Termed “Ecological Intensification” (Tittonell 2014), this alternate model of agricultural management contributes to achieving farmer’s goals through ecosystem services that replace or augment fertilizer and pesticide inputs (Kleijn et al. 2019) and encourages management practices that reflect natural cycles, such as crop rotation or dynamic landscapes that include both crops and natural habitats (Geertsema et al. 2016).

Carabids and their Role within Agricultural Landscapes

The primary focus of my research and this review will be on ground beetles, or carabids (Coleoptera: Carabidae), and what factors that contribute to their community composition and provision of ecosystem services. Carabidae is the 3rd largest family of beetles in North America with greater than 2,600 species, 400 of which are well known in agricultural landscapes (Lindroth 1961-1969; Goulet et al. 2002). They range from a few millimeters (*Stenolophus species*) to over 40 millimeters (*Carabus species*). Adults are easy to recognize with their streamlined, dark or metallic bodies, grooved elytra, and long legs adapted for running and burrowing (Lindroth 1961-69; Lovei and Sunderland 1996). Most carabids are nocturnal and have dark coloring compared to the iridescent or metallic coloring of diurnal species; however, their activity can change depending on habitat, time of year, or microclimatic conditions (Lovei and Sunderland 1996).

In Carabidae, overwintering stage and timing of reproduction are linked, with species overwintering as adults typically reproducing in the spring (spring breeders), and those overwintering as larvae reproducing in the fall (autumn breeders) (Lindroth 1961-69; Lovei and Sunderland 1996). Carabids typically have three larval instars, although the genera *Harpalus* and *Amara* have two (Lindroth 1961-1969; Lovei and Sunderland 1996).

Overwintering characteristics vary by species locally and regionally. Adult overwintering species emerge early in the spring to colonize fields, scout for prey, and mate; whereas larval overwintering species emerge as adults and colonize the area later in the field season (Lindroth 1992; Lovei and Sunderland 1996). Overwintering location and depth of the burrow are dependent on soil properties such as moisture and texture but are also influenced by habitat disturbance (Holland and Luff 2000). Beetles vary in burrow depth across and within species; for example, *Harpalus pensylvanicus* DeGeer burrows can range from 5-15 cm deep (Kirk 1973) as compared to *Harpalus rufipes* DeGeer which reaches 45 cm (Kulkarni et al. 2015). Generally, ground beetles live only one year and are univoltine; however, larger species or autumn-breeders have been known to survive longer in laboratory conditions and multi-annual cycles can occur in extreme environments (Lovei and Sunderland 1996).

Common predators of carabids include birds, small mammals (rodents), arthropods, or even other carabids. Holland (2002) provides an excellent review of the literature on carabid natural enemies but ultimately determines that potential predation by birds and mammals is not significant enough to impact carabid populations in agroecosystems. However, several studies provide evidence that shrews (Churchfield 1982) and field mice (Green 1979) are the top predators of invertebrates such as carabids in arable fields. Carabids are most vulnerable to predation as larvae but are generally protected within underground burrows (Holland 2002).

Dispersal ability in carabids is important for colonizing new habitats and expanding their predation potential, particularly within large monocultures of row crops. Although most are winged, running is a more common and efficient form of movement. Flight is dependent on habitat quality and level of disturbance, as stable environments lead to a lower proportion of winged individuals (Lovei and Sunderland 1996). Beetle size can also affect the distance of dispersal, as larger beetles have larger home ranges and typically reduced flight ability. One study found *Pterostichus melanarius* Illiger, a non-native predator in grassland and agricultural systems of the US, could travel 55 meters by ground over the course of 30 days (Thiele 1979; Holland and Luff 2000). Dispersal is considered “random” for most carabids, rather than directed towards more favorable habitat conditions or food resources (Lovei and Sunderland 1996). Therefore, the configuration of habitats within an agricultural landscape is important in shaping where and to what extent carabids beetles colonize an area.

Use as Bioindicators

Understanding and evaluating the impacts of managed landscapes on biodiversity and ecosystem health is important for conservation or mitigation efforts. One way to measure biodiversity is through bioindicators, i.e., species or taxa that are sensitive to changes in environmental condition and whose behavior or species assemblage may represent the change in biodiversity across multiple taxa in that ecosystem (Niemela 2000; Lindenmayor et al. 2001). Carabids are useful bioindicators as their taxonomy and biology are well known, they are globally abundant as either specialists or generalists in various habitats, and they are relatively easy to sample (Lovei and Sunderland 1996; Rainio and Niemela 2002). In row crop agriculture, Carabid species assemblages and abundance are indicative of agronomic management practices (Carcamo et al. 1995; Clark et al. 1997; Burglo et al. 2015) or the size and distribution of non-crop habitat within the landscape (Rischen et al. 2021; Knapp et al. 2022).

Role as Insect Predators

Carabids are primarily opportunistic, polyphagous predators or scavengers that use sight or volatile compounds to hunt for prey (Lovei and Sunderland 1996). In Europe and North America, studies have shown that ~ 92% of recorded species are predaceous or omnivorous, although this frequency varies by habitat or available prey (Lovei and Sunderland 1996). Common prey includes aphids, slugs, leafhoppers, springtails, thrips, the adults and larvae of Lepidoptera, as well as spiders or other non-insect arthropods; larger species have been known to also eat smaller beetles (Lindroth 1961-69; Lovei and Sunderland 1996; Kirk 1973). In most European and North American croplands, carabids can provide efficient pest suppression to avoid pest outbreaks (see review by Kromp 1999); however, other ground-dwelling arthropods such as Opilionids, spiders, and ants are necessary to sustain pest suppression throughout the growing season (Lovei and Sunderland 1996).

Role as Seed Predators

Although most carabids are polyphagous predators, there are species that prefer or specifically consume seeds (granivores) and plant material (herbivorous). Carabids are opportunistic feeders, and even predaceous adults or larvae will exhibit granivorous habits in the absence of prey in early spring, as seeds provide high levels of protein and nitrogen; in general, Carabid diets can be complex and have not been thoroughly studied, particularly for larvae (Lovei and Sunderland 1996; Lindroth 1961-1969; Kulkarni et al. 2015). Carabids are important

for weed seed suppression in row crops, as they consume post-dispersal seeds on the surface and those buried by mechanical tillage (Kulkarni et al. 2015) and have been found to regulate the weed seedbank in multiple row crop systems (Bohon et al. 2011). Behaviors associated with granivorous beetles also include pre-dispersal seed predation (climbing of plants to consume flowers or seeds), and caching seeds in burrows for their larvae (Kulkarni et al. 2015). Seed preference is dependent on body size, with larger beetles consuming larger seeds and exhibiting preferences that could shape interactions within the weed and granivore communities of a site over the long-term (Honek et al. 2007; Gaines-Day and Gratton 2010; Kulkarni et al. 2015). Predatory species are more commonly found in open-ground habitats with or without plant cover, while phytophagous species are associated with habitats with high plant diversity or density (Lovei and Sunderland 1996; Harvey et al. 2008). In a three-year study in the Netherlands, Harvey et al. (2005) found that Carabid community composition in agricultural landscapes have become dominated by phytophagous species, regardless of cropping treatment. Although the reason for this is not entirely known, the authors suggest that structural diversity of vegetation in the plot is a primary driver. This is supported by a study in Sweden that found high crop diversity in the previous season was a greater driver of Carabid diversity than the current field conditions (Raderschall et al. 2022).

Abiotic and Biotic Factors affecting Carabid Communities

Climate Change and Phenology

Climate change will most likely impact arthropod abundance and diversity in agroecosystems as we continue to see increased temperatures and shifting rainfall patterns; however, relatively few studies have investigated the long-term effects of climate change on carabids. A 16-year study in Europe found that Carabid tolerance to temperature range is correlated to the rate of species turnover; such that communities dominated by specialists with a limited temperature niche will experience turnover much faster (Bowler et al. 2015). However, in this experiment, temperature niche was associated with species diversity and not population change. An experiment by Zaller et al. (2014) predicted that expected rainfall patterns in Germany will lead to 25% more dry days and an overall reduction in accumulated rainfall, thus impacting overall soil moisture and weed density. Conversely to Bowler et al. (2015), the trends found in Zaller are expected to impact arthropod population abundance, rather than species diversity. Carabids have also been found to be early indicators of microclimatic conditions in a

30-year study of the low-elevation Italian Dolomites, as species turnover in their communities occurred at a faster rate than plants (Pizzolotto et al. 2014; Brandmayr and Pizzolotto 2016). As ice retreated with warming temperatures at high elevations, ground beetles were quick to colonize the early successional habitats that developed; subsequently, generalist species with a greater temperature tolerance and high dispersal ability became dominant in these new communities. Dispersal may be a key factor impacting ground beetles in the face of climate change. In a similar study in the Dolomites, Brandmayr and Pizzolotto (2016) found that forest communities remained largely the same, whereas grassland communities experienced high turnover, compensating for the effects of climate change. As forests will likely be subjected to changing temperatures, species with low dispersal ability will be unlikely to adapt. As no studies have investigated the impacts of climate change on Carabid assemblages in agricultural fields of the Midwest, US, we do not know how carabids will react to climate change here, but the changes in microclimate may likely favor dominance of a few generalist species tolerant of arid conditions and high disturbance.

Carabids are spatially and temporally diverse: emerging, mating, hunting, and laying eggs throughout the growing season. Communities within the same location may support many rotations of emergence, dependent on the available food supply and climatic conditions. A study on the phenology of carabids found that increasing daily temperatures due to climate change may be leading to earlier emergence times for spring breeders, resulting in an extended season for mating and foraging; however, early emergence may also place these beetles at risk of inconsistent spring weather (Pozsgai and Littlewood 2014). Conversely, later emergence by autumn breeders to avoid high mid-season temperatures may be beneficial but could reduce the length of their season for mating, foraging, and laying eggs (Pozsgai and Littlewood 2014).

Landscape

Landscape characteristics influence the community composition and population size of carabids within agricultural landscapes. Within-field dynamics such as temperature, humidity, and vegetation density are related to agricultural practices (Raderschall et al. 2022) and could influence local communities; however, the extent of existing populations within the greater landscape may influence the capacity for diversity within fields (Pulliam 1988; Hanski and Simberloff 1997). Filter theory suggests that the abiotic characteristics of an environment, such as human modification of crop fields that reduce vegetative diversity and foster arid conditions,

may result in the exclusion of species (Kraft et al. 2015, Cadotte and Tucker 2017). In agricultural landscapes, this is characteristic of “sink” habitats or isolated patches where the local conditions cannot support stable populations, and without reintroduction from nearby habitats would result in local extinction (Pulliam 1988). Whereas the isolation of patches may have “sink” properties, the distribution of patches within a site creates dispersal networks between populations and contributes to the greater metapopulation of an agricultural landscape (Gilpin and Hanski 1991; Hanski and Simberloff 1997). However, the conversion of diverse landscapes to intensively managed row crops removes connecting features such as hedgerows, forests, or riparian areas that facilitate dispersal and provide necessary habitat for foraging or overwintering, further limiting the potential for biodiverse communities (Tewksbury et al. 2002; Tscharnkte 2005; Tscharnkte et al. 2012). Arthropods are limited by their dispersal ability, especially ground dwelling beetle species that are incapable of flight such as *Cyclotrachelus sodalis* LeConte, or smaller species with reduced home ranges such as *Elaphropus anceps* LeConte (Lindroth 1961-1969). When semi-natural lands or non-crop areas are increasingly isolated from surrounding diverse landscape features, the diversity of those patches is reduced, as is their potential to contribute to arthropod populations within row crops (Gardiner et al. 2010; Tscharnkte 2005; Landis 2017). Further, the homogenization of landscapes is also contributing to the homogenization of species, towards generalist over specialist diets and habitat preferences (Dolezal et al. 2022). Ground beetle communities within row crops then, are dependent on the local landscape to support their population stability and potential biodiversity (Pulliam 1988; Tscharnkte 2005; Tscharnkte et al. 2012), and the influence of the available species pool may be greater than agronomic practices within row crops (Tscharnkte 2005; Tscharnkte et al. 2012).

The introduction of refuge habitats distributed throughout simplified landscapes may help mitigate the isolation and diversity of Carabid communities. As such, simplified rather than diverse landscapes derive greater benefit from conservation practices that broaden the available species pool (Tscharnkte et al. 2005, 2012; Knapp et al. 2022). Further, providing a variety of refuge sites in the form of polyculture grasslands, prairies, and forests evenly distributed across the agricultural landscape will increase “connectedness between patches” for arthropod predators (Gardiner et al. 2010). The “intermediate habitat complexity hypothesis” described by Tscharnkte et al. (2005) suggests that increasing the diversity of agricultural landscapes via edge

or refuge habitat results in greater diversity than either complex or simple habitats. Several studies support this hypothesis, as transition zones between forests or grasslands with row crops result in higher Carabid abundance than within the row crop alone, although not at the extent of the forest or grassland (Thomas et al. 2002; Knapp et al. 2022). Restored semi-natural lands are therefore useful in improving Carabid biodiversity within agricultural landscapes, at practical temporal and spatial scales for easy farmer adoption.

Crops and Rotations

Crop selection and rotation may influence the community of carabids present within an agroecosystem. In the US Midwest, row crop agriculture typically follows a corn-soybean or corn-wheat-soybean rotation. Carabid activity is dependent on multiple environmental factors, the most important of which are humidity and light at the soil surface (Thiele 1979). Corn and wheat provide less shade cover, which may contribute to increased temperatures and reduced soil moisture at the surface where carabids nest or hide during the day, particularly during the earlier phases of crop growth in May-June. In comparison, the dense vegetation of soybean could provide better cover and protection from both environmental factors and predation. In a study on a diverse cropping system that included legumes, vegetables, and cereal crops, Eyre et al. (2012) found that beans harbored the greatest diversity, although greater abundance or instances of aggregation behavior were found in cereal crops like wheat or barley (*Hordeum vulgare* L.). A study in several habitats in Iowa, including grasslands, row crop (oat (*Avena sativa* L.), soybean, and corn), prairie, and woodland found that diversity within grasslands and prairie were highest and supported the most specialists, followed by woodland and lastly, row crop (Larson et al. 2002). Most of the beetles found within the row crops were in soybean as compared to oat or corn; yet oat had similar habitat characteristics to the prairie and hosted similar ground beetle communities (Larson et al. 2002). Despite this, other studies (Carcamo and Spence 1994; Clark et al. 1997; Clark 1999; Eyre et al. 2012; O'Rourke et al. 2008) have demonstrated that crop type does not contribute to long-term community composition or abundance, and instead management practices have the greatest impact.

Crop Management

Agronomic practices such as tillage or pesticide applications may influence Carabid fitness, composition, and efficiency as natural predators and granivores within row crops. Tilling or plowing are common agricultural practices that mechanically disturb the top layers of soil to

prepare the seed bed and reincorporate soil residue, while also helping to manage weeds. Many types of tilling practices are available, that range from deep moldboard plowing (> 25 cm) to shallow-till (5-10 cm) or conservation-oriented in the form of no-till or strip-tilling (shallow tillage within seeding rows) (UMN extension n.d.). Consistent tilling of arable land may lead to reduced water holding capacity, nutrient runoff of the fine top soil, and less organic matter within the soil; all of which can be damaging to yield in the long-term, but also to burrowing or ground-dwelling arthropods within row crops. Carabids, like many insects, are vulnerable to disturbances that alter temperature and humidity (Thiele 1979; Lovei and Sunderland 1996). As ground-dwelling arthropods, they often hide within cracks or holes in the soil during the day to avoid high temperatures and overwinter by burrowing into the soil in the fall. Burrows range in depth depending on species and typically consist of either an adult or larvae secured with a food source (Lindroth 1961-1969; Kirk 1973; Lovei and Sunderland 1996). Consistent tillage may deter many carabids from burrowing within crop fields or reduce the carrying capacity of the field to support large overwintering populations. Tilling or plowing either occur in the spring before seeding the crop, or in the fall after harvest; as such, this disturbance may directly damage the vulnerable adult or larval overwintering stages (Kladivko 2001; Muller et al. 2022).

Although no-till practices maintain soil moisture and encourage ground-dwelling arthropod activity, the trade-off is that weed control is reliant on herbicides. Reduced tillage practices encourage greater species richness and abundance of carabids than plowing; however, different variations of tillage techniques also favor different communities (Anderson 1999; Muller et al. 2022). Available crop residue on the soil surface, which is higher in no-till than shallow or plowing where it's incorporated back into the soil, increases soil moisture and humidity while decreasing temperatures at the surface. This may favor some Carabid species that prefer moist conditions, as compared to species common to agricultural fields such as *Agonum placidum* Say or *Poecilus chalcites* Say that prefer dry, arid conditions attributed to tilling (Lindroth 1961-1969). Weed density, an indirect effect of tilling practices, also influences the communities of carabids within crops and may be more important for some species assemblages than the effects of tilling alone (Anderson 2003). Other indirect effects include available prey that favor either moist conditions of high soil residue or weed cover, such as slugs (Mueller et al. 2022), a common prey to *P. melanarius*, a non-native predator that also consumes smaller carabids (intraguild predation) and dominates agricultural studies of the Midwest, US, and southern

Canada (Carcamo et al. 1995; Larsen et al. 2002).

Cover cropping is a common technique used to improve soil quality by providing plant cover year-round. The effect of cover cropping on Carabid species assemblage or abundance has not been extensively studied. In a study on intercropping canola and wheat, Hummel et al. (2012) did not find any significance for beetle diversity. Double-cropping is another method intended to diversify the field, while also increasing yield on limited land. A study in Germany on double-cropping pennycress (a biofuel crop) with corn resulted in increased Carabid abundance and diversity as compared to fallow-corn rotations (Groeneveld and Klein 2015). The authors suggest that plant cover in winter and early spring contributed to this result, as well as the later sowing time for the pennycress-corn system.

Fertilizers

Few studies have compared the direct impacts from fields amended with inorganic fertilizer as compared to organic amendments such as manure or compost, although many studies compare conventional to organic or reduced agronomic practices on Carabid assemblages (Carcamo et al. 1995; Clark 1999; Holland and Luff 2000; O'Rourke et al. 2008; Rossi et al. 2019). Available supply of compost in the spring from the application of fall manure appeared to have a greater impact on spring breeders than the addition of soil amendments alone (Hance and Gregoire-Wibo 1987). Any introduction of soil amendments is likely to influence vegetative density, either as weeds or crop, and impact the microclimate at the field scale; further, organic matter inputs influence the microbial community and contribute to a diverse food supply to support Carabid communities (Clark 1999; Holland and Luff 2000; Mueller et al. 2022).

Chemical Pesticides

Agrochemical applications are of particular concern for carabids. Applications of herbicides change plant cover and remove food resources for weed seed eaters, while insecticides can reduce prey items for generalist predators (Holland and Luff 2000). Application over many years may also filter prey communities, further limiting the diversity of arthropod communities present on the landscape. The available literature on pesticides in agricultural landscapes warrants further study on the impact to carabids, among other beneficial arthropods; here, I review direct and indirect impacts of pesticides on Carabid communities.

Fungicides

Few studies have investigated the impacts of fungicides on carabid health or function.

However, indirect effects of fungicide applications can disrupt or reduce arthropod predator communities through prey mortality, as carabids are known to feed on fungivores such as collembola (Lindroth 1961-1969; Dubey et al. 2020). In a lab experiment, carabids exhibited limited susceptibility to direct exposure of fungicides and of the 18 species studied, only *Scarites quadriceps* (Chaudoir) displayed some vulnerability (Mullin et al. 2005). However, treated seeds often combine insecticides with fungicides, which have been documented to impair carabids after ingesting exposed prey (Douglas et al. 2015).

Herbicides

The advent of herbicide resistant crops has fundamentally changed Midwest row crop systems, with implications for Carabid communities. Prior to the availability of glyphosate-resistant soybeans and corn, weed control was achieved by a combination of rotations, tillage, pre- and post-emergence herbicides, and mechanical cultivation; even with herbicide application, mechanical practices are still necessary today (Ghersa et al. 2000). Herbicide-resistant crop varieties have simplified weed control in corn and soybean, but the emergence of weed resistance continues to challenge growers. Herbicides have not been documented to impact carabids through direct toxicity such as with insecticides (Mullin et al. 2005), but the indirect effects of reduced weed density and habitat has been found to affect obligate granivores, especially larger beetles that prefer dense, vegetative structure (Holland and Luff 2000; Kulkarni et al. 2015). Multiple studies have attributed higher species diversity of carabids, particularly granivores, to agronomic practices that limit soil disturbance and herbicide application (Carcamo and Spence 1994; Clark 1999; Harvey et al. 2008).

Insecticides

Like herbicide resistant crops, genetically-modified insect resistant crop varieties have greatly changed insect management practices in the Midwest US. Prior to the advent of these varieties, insect management was achieved by a combination of tolerant varieties and cultural controls (e.g., crop rotation), coupled with scouting and treatment if thresholds were exceeded. For example, the European corn borer (*Ostrinia nubilalis* Hubner) had been a serious pest of corn since the early 1900's regularly requiring applications of organophosphate or synthetic pyrethroid insecticides to achieve acceptable control (Hill et al. 1967). With the advent of genetically modified corn varieties expressing Cry1-based toxins of the soil bacterium, *Bacillus thuringiensis* Berliner (Bt), corn became essentially immune from corn borer attack and farmers

rapidly adopted the technology (Zwahlen and Andow 2005; Bessin et al. 2019). Similarly, Northern and Western corn rootworms (*Diabrotica barberi*) and *D. virgifera virgifera* LeConte) respectively, were major pests of corn requiring the use highly toxic carbamate and organophosphate soil insecticides. Bt transgenic corn expressing Cry3toxins targeted to coleopteran pests has largely eliminated rootworms as serious pests (Zwahlen and Andow 2005).

Other synthetic pesticides with reduced risk to humans have been developed and become common in row crop agriculture. Neonicotinoids are a systemic insecticide often used as a seed coating on Bt transgenic corn and occasionally as a foliar application (Mullin et al. 2005; Hall et al. 2022). These include the chemicals imidacloprid, thiamethoxam, and its resulting metabolite, clothianidin (Mullin et al. 2005; Gasparic et al. 2022). Neonicotinoids are a controversial insecticide and have been banned in the United Kingdom and European Union under concern for non-target effects on pollinators (Goulson 2013; Gasparic et al. 2022). Debate on the effect of neonicotinoids as the sole factor leading to bee mortality continues (Goulson 2013; Lundin et al. 2015), but the current consensus suggests a multitude of factors including pathogens and viruses that, when combined with pesticide exposure, may lead to greater vulnerability to individual foraging bees (Goulson 2013; Doublet et al. 2015).

Non-target effects of neonicotinoids on beneficial insects include exposure of nearby wildflower refugia or field edges to the dust produced by neonicotinoid coated seeds during sowing (Goulson 2013; Hall et al. 2022) or eventual uptake by plants downstream of crop fields (Hall et al. 2022). In a study by Hall et al. (2022) in croplands of Iowa, two neonicotinoid chemicals imidacloprid and thiamethoxam were detected in over 90% of all soil samples and clothianidin was detected in 100% of samples. To test for exposure of natural refugia nearby to neonicotinoid treated agricultural fields, Hall et al. sampled milkweed and found presence of at least one neonicotinoid chemical in ~80% of all samples. Another study by Humann-Guillemot et al. (2018) sampled a gradient of intensive agricultural management in southern Sweden and found that 93% of organic fields had soil residues of at least one neonicotinoid despite the lack of neonicotinoid application in those fields. Further, they found 87% of commercial, organic crop seed had neonicotinoid residues, proving just how widespread the use, and consequently, the impact of neonicotinoids across the global, agricultural landscape.

The non-target impacts of neonicotinoids, Bt transgenic corn, and other synthetic insecticides have been evaluated for Carabidae, who as natural predators and scavengers, are

vulnerable to direct toxic exposure, consumption of intoxicated prey, and loss of prey abundance. Multiple studies have found that Bt transgenic corn, including the Cry3-based toxins that target coleopterans, have little to no effect on ground beetles (Mullin et al. 2005; Leslie et al. 2009; Twardowski et al. 2017). However, neonicotinoids, which are often applied as seed coatings for Bt transgenic corn, can have adverse effects on carabids. In a laboratory study, high concentrations resulted in near 100% mortality in 17 of the 18 species of carabids tested (Mullin et al. 2005). The authors found a delay in beetle symptoms after ingestion of neonicotinoid-exposed prey up to four days, but this varied by species. Of those tested, *P. chalcites* and *H. pensylvanicus* were noted as the most tolerant of both fungicide and neonicotinoid exposure, and most recovered from paralysis. However, in a field setting, paralysis would most likely result in mortality from opportunistic predation, such as ants, as Mullin et al. (2005) noted from field observations. Indirect exposure to insecticides, either through ingestion of exposed prey or prey that has fallen after a foliar application is the most likely non-target effect on carabids. In a study on the grey garden slug (*Deroceras reticulatum* Muller), an agricultural pest in soybean crops, the slugs were not affected by ingestion of neonicotinoid coated seeds, however, over 80% of the carabids that consumed the exposed slugs experienced some adverse effect (Douglas et al. 2015). It is unknown how long-term use of neonicotinoids and soil residues will impact carabids. A study in Croatia on neonicotinoid use in sugar beet crops found a high prevalence of neonicotinoid residues in carabids collected; however, all residues were considered below lethal amounts (Gasparic et al. 2022).

Indirectly, the loss of prey from pesticide use could also contribute to changes in arthropod predator communities. In a study on the effects of pesticide use on Carabid activity-density and composition in fields with and without refuge sites, Lee et al. (2001) found that Carabid communities did functionally shift after pesticide applications towards refuge sites due to reduced prey availability in the field. They also noted that reduced activity-density persisted into late summer for fields without refuge strips, as application of spring pesticides likely impacted the vulnerable larval state of beetles in the soil. Conversely, one study found that applications of either pyrethroids or neonicotinoids resulted in a 16% decline of carabids but not spiders or mites. The authors suggest that available prey populations were suitable to maintain natural predators, and instead the direct effects of pesticides impacted the Carabid population (Douglas and Tooker 2016).

Conservation Practices to Conserve Carabid Communities

In some European countries, on-farm habitats are specifically managed to enhance carabids and other arthropod natural enemies by providing food, nesting sites, and reduced disturbance from farming practices (Holland and Luff 2000). One practice termed “beetle banks” is managed to encourage beetles to overwinter within fields, emerging the following season to act as beneficial predators within row crops. Beetle banks are favored by adult overwintering species that would be vulnerable to tilling or disturbance within the field and emerge in the early spring to colonize row crop pests (Holland and Luff 2020). Traditional beetle banks run the length of a field or boundary and consist of a raised mound of earth roughly 40 cm high, planted with tussock-forming grass species favored by some predatory beetles and spiders (Macleod et al. 2004). The placement of beetle banks is crucial, as beetles are known to travel limited distances (dependent on size and availability of prey items) from their source habitat. Carabids are often found within 60 m of their overwintering habitat and decrease in species richness with distance (Holland et al. 1999). Beetle banks also encourage nesting habitat for game birds, pollinators, and other wildlife (Holland et al. 1999). Hedgerows, in comparison, are narrow strips usually placed along the outside of the field or between fields and consist of opportunistic or managed grasses, wildflowers, shrubs and trees.

In the US, similar semi-natural habitats, such as restored grasslands and fencerows, have the potential to support a wide diversity of beneficial organisms and ecosystem services. Increasing the complexity within the agricultural landscape to include semi-natural lands may encourage the spillover of these services to the row crop (Tscharntke et al. 2005; Gardiner et al. 2010; Robinson et al. 2021). Incorporating semi-natural land and conserving grasslands have proven to provide sources of overwintering of carabids, through a diversity of available plant material and protection from disturbance common in the row crop, while increasing the resilience of predator communities to agronomic disturbance (Carmona and Landis 1999; Lee et al. 2001; Massaloux et al. 2020; Rischen et al. 2021).

Prairie Strips

Developed by researchers at Iowa State University, the Science-based Trials of Row-crops Integrated with Prairie Strips project (S.T.R.I.P.S.), utilizes strips of perennial prairie grasses and flowers to reduce soil erosion and water pollution (Schulte et al. 2017). Strips are strategically positioned to slow water movement, increase infiltration, and retain nutrients, with

runoff of sediment, phosphorus, and nitrogen reduced by 1.6 times compared to fields without strips (Schulte et al. 2017). Prairie Strips also improve wildlife habitat harboring 2.6 times greater number of insect taxa overall, and greater than twice the number of pollinator and natural predators than fields without strips (Schulte et al. 2017). Arthropod natural enemies benefit from semi-natural land such as field margins, beetle banks, and prairie strips within intensive row-crop agriculture, as it serves to diversify the landscape and provide refuge from disturbance or pesticide use, as well as resources for overwintering and alternative prey not found in the crop field (Lee et al. 2001; Massaloux et al. 2020; Robinson et al. 2021).

CONCLUSION

Agricultural landscapes are currently designed for high input, high productivity cropping systems that may not be ecologically, economically, or socially sustainable. Simplifying diverse landscapes limits dispersal of communities, colonization of new habitats, and the resilience of agroecosystems; as providers of ecosystem services that regulate and support crop yield, the conservation of natural systems and beneficial arthropods is of high priority to some farmers. Carabids are beneficial native predators within row crop agriculture and serve as useful indicators of biodiversity across agroecosystems. Traditional agricultural management factors that contribute to their fitness, efficiency as service-providers, and community composition include soil amendment and disturbance, crop type, and pesticide application. However, the distribution of semi-natural habitat across agricultural landscapes may support a more diverse community of natural predators. Including perennial prairie strips within traditional row crop agriculture, alongside conservation-oriented practices such as reduced tilling or pesticide use, may improve overwintering habitat for carabids and other natural predators, and enhance natural pest suppression within agroecosystems.

Mitigating the current and historical impacts of agricultural management will require a collaborative effort between farmers and the farming community, academic researchers, and policy-makers. Prairie strips are a low-maintenance solution that can be widely adapted to fit farmers' needs and that of the local landscape. Sustainable food systems will require conservation and collaboration to achieve solutions to landscape scale biodiversity and habitat loss, and support thriving communities – people and nature alike.

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CHAPTER TWO: LONG-TERM AGRICULTURAL MANAGEMENT REDUCES ABUNDANCE AND ALTERS COMMUNITY STRUCTURE OF GROUND BEETLES (COLEOPTERA: CARABIDAE)¹

ABSTRACT

Carabid beetles (Coleoptera: Carabidae) are beneficial predators in agricultural landscapes. We studied changes in community composition, activity-density, and diversity of carabids in a long-term agroecosystem study spanning 30 years in the US Midwest. We contrasted carabid community metrics measured by pitfall trap sampling in two conservation-oriented treatments in a corn-soybean-wheat rotation. One treatment uses conventional practices but with reduced agrochemical inputs (Reduced Input), while the other has no synthetic inputs (Biologically Based). Since a 1994-95 study on the same site, in 2019 overall carabid activity-density had declined a minimum of 58-76% with the four previously dominant species (all predators) declining 94-98% and becoming uncommon to rare. In addition, carabid species richness, activity-density, and community structure have diverged significantly under the two management regimes. In 2019 sampling, activity-density decline in the Biologically Based treatment was mitigated by large increases in the abundance of two granivorous species (*Harpalus compar* (LeConte) and *Harpalus pensylvanicus* (DeGeer)). In contrast, carabid activity-density in the Reduced Input treatment remained low. After decades of management, the Biologically Based treatment supported greater diversity and activity-density of carabids compared to Reduced Input, and community structure shifted from predatory toward granivorous species. This long-term study contributes to the growing literature on insect decline in agricultural landscapes and demonstrates that changes in abundance and species turnover of the carabid communities can occur even under conservation-oriented management regimes.

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INTRODUCTION

Insects are primary providers of ecosystem services in agroecosystems via contributions to decomposition, pollination, and suppression of crop pests. However, current research on long-term insect population trends indicates a global decline (Wagner et al. 2021); for example, with a 75% decline in flying insect biomass in some agriculturally dominated landscapes (Hallmann et al. 2017). Agriculture currently occupies 40% of the global terrestrial land base (Sustainable Food and Agriculture 2020). To meet the demand of a growing human population, agricultural production has become increasingly efficient through advancements in farming equipment, pest management, and high yielding commodity crops. However, land use change resulting from the intensification and expansion of agriculture have led to landscapes dominated by high-input row crop monocultures, contributing to the loss of biodiversity (Tscharntke et al. 2012) and reductions in ecosystem services that maintain air, water, soil health, and crop productivity over the long-term (Daily 1997; Chee 2004). Climate change, habitat loss or isolation of semi-natural lands in agroecosystems, and widespread use of agrochemicals are all likely contributors to the decline in beneficial insect biodiversity and provision of services (Bianchi et al. 2006; Tscharntke et al. 2012; Hallmann et al. 2017; Wagner et al. 2020; Rischen et al. 2021). Ground beetles or carabids (Coleoptera: Carabidae) are common beneficial predators in agricultural landscapes and can be indicators of ecosystem change. Carabids consume agricultural pests such as aphids, slugs, the adults and larvae of Lepidoptera, as well as spiders or other non-insect arthropods (Lovei and Sunderland 1996; Lindroth 1961-69; Kirk 1973). Although most carabids are polyphagous predators, some species primarily consume seeds (granivores) or plant material (herbivores) (Lovei and Sunderland 1996; Lindroth 1961-1969). Carabid populations are sensitive to changes in environmental conditions, the most important of which are humidity and light at the soil surface (Thiele 1979). In row crop agriculture, carabid species assemblages and activity-density are indicative of agronomic management practices (Carcamo et al. 1995; Clark et al. 1997) and thus serve as bioindicators for diversity of other ground-dwelling arthropods (Lovei and Sunderland 1996; Rainio and Niemela 2002). Studies of ground beetles in agroecosystems have previously examined how crop type (Rivard et al. 1966; Carcamo and Spence 1994), management (Allen 1979; Carcamo et al. 1995; Clark et al. 1997; Clark 1999; Holland et al. 1999; Thomas et al. 2002; Cox et al. 2014), or conservation practices (Middleton and MacRae 2021; Rischen et al. 2021; Knapp et al. 2022) impact their overall

activity-density, diversity, community composition and predation potential. Production of corn (*Zea mays*, L.), soybean (*Zea mays* L. – *Glycine max* L.), and to a lesser extent wheat (*Triticum aestivum* L.) dominate agricultural landscapes of the Midwest, US. How these annual cropping systems are managed can influence carabid biodiversity and community structure. Although crop type may influence the microclimate of a field, multiple studies have demonstrated that the crop present in a given year does not strongly influence long-term carabid community composition or activity-density, and instead management practices have the greatest impact (Carcamo and Spence 1994; Clark et al. 1997; Clark 1999; Eyre et al. 2012; O’Rourke et al. 2008). For instance, tillage practices redistribute topsoil which could disrupt overwintering ground beetles (Kirk 1973; Knapp et al. 2022) and within annual cropping systems, might filter for a community of carabids with high tolerance to soil disturbance (MacLeod et al. 2004). Weed density, which is shaped by tillage practices and herbicide use, also influences carabids that feed on weed seeds (granivores) and may be more important for some species assemblages than the impacts of tillage alone (Anderson 2003). Agricultural pesticides, including the use of Bt transgenic corn, neonicotinoid-coated seeds, and fungicides, have been found to influence the overall activity-density of ground dwelling arthropods (Mullin et al. 2005; Goulson 2013; Douglas et al. 2015; Douglas and Tooker 2016), and subsequently their ability to suppress pests (Douglas et al. 2015). These and other factors may be key in understanding the effects of long-term management on community composition of carabids in annual cropping systems.

Long-term studies in agriculture, defined as more than 20 years in duration (Rasmussen et al. 1998) can provide unique insights into ecosystem change (Bahlai et al. 2021). The Long-Term Ecological Research (LTER) Main Cropping Systems Experiment (MCSE) at Kellogg Biological Station (KBS), Hickory Corners, Michigan was established in 1989 and compares crop management practices across a gradient of low to high management intensity (Robertson and Hamilton 2015). Given the importance of carabids in agroecosystems, and their potential as indicators of agricultural disturbance, carabid communities were first studied in 1994-95, five to six years after the experiment was initiated (Clark et al. 1997), and again in 2019 after 30 years of continuous management. Here we focus on two annual row crop treatments within the MCSE, one representing conventional agriculture with reduced pesticide and fertilizer inputs (Reduced Input) and a second treatment (Biologically Based) with no synthetic inputs and minimal fertilizer application (Robertson and Hamilton 2015). Our objectives were to first characterize

any changes in overall carabid abundance (as measured by activity-density) during the 25 years between the studies, and secondly to contrast carabid activity-density, community structure, and feeding guilds resulting from the long-term application of the management regimes. We did not have *a-priori* predictions on how carabid communities may change over the 25-year period, in large part because such studies are rare, but predicted that long-term management under conservation-oriented management practices would result in distinct communities of carabids that differ in terms of diversity, activity-density, and community composition.

MATERIALS AND METHODS

Study System

This study was conducted in 2019 at the Kellogg Biological Station, Long-Term Ecological Research site (KBS-LTER) in Hickory Corners, Michigan (42.411078, -85.377195). The KBS-LTER Main Cropping Systems Experiment (MCSE) was initiated in 1989 and includes continuously managed treatments representing a gradient of management intensity from conventional to minimal input in an annual corn-soybean-wheat rotation. Each treatment is replicated $n=6$ times in 0.88 ha plots (87 m x 105 m) in a randomized complete block design (Figure 2.1). Corn and soybean are planted in the spring while wheat is planted in the fall following soybean harvest and harvested mid-July of the following year (Robertson and Hamilton 2015).

In 2019, the MCSE had been in place for 30 years allowing us to investigate the long-term effects of two conservation-oriented management regimes on carabid communities. The Reduced Input treatment receives approximately one-third the rate of synthetic chemical inputs (fertilizers and pesticides) as conventional management practices, whereas the Biologically Based treatment does not receive any synthetic pesticides with minimal fertilizer input to periodically adjust for crop removal. Following corn and wheat harvest, both treatments are chisel-plowed, and soil finished before seeding winter cover crops. Cereal rye (*Secale cereale* L.) is planted following corn, and medium red clover (*Trifolium pratense* L.) following wheat. Because wheat is fall-planted after soybean harvest, no additional cover crop is planted. In corn and soybean years, the Reduced Input treatment receives pre-emergence herbicides and is rotary-hoed and cultivated as necessary to further control weeds. The Biologically Based treatment receives no herbicides and relies exclusively on cover crops, rotary-hoeing, and cultivation for weed control. While the overall management goals for each treatment have remained in place

since inception, the products applied (rates and application dates) have shifted to reflect current local practices and to address nutrient deficiencies and pest outbreaks. Details of the fertilizer and chemical applications in 2018-2019 are found in Supplemental Information (Table 2.1) with the full agronomic catalog available at the KBS-LTER website (*kbs.lter.msu.edu*).

A new USDA-sanctioned conservation practice CP-43 Prairie Strips (USDA FSA 2019; USDA NRCS 2020) was implemented in the Reduced Input and Biologically Based treatments in 2019. Prairie Strips have previously been documented to increase biodiversity and to reduce soil and nutrient runoff in annual cropping systems (Schulte et al. 2017). Specifically, a mixture of native, warm season grasses and forbs (4 grass species, 18 forb species; see Kemmerling et al. 2022) (Table 2.1) were seeded in 5 x 105 m areas in the middle of each plot, dividing the cropped area into two halves lengthwise. Plots were seeded on 25 April 2019, with an oat (*Avena sativa* L.) nurse crop and mowed in late July. Because the seeded native perennials are slow to establish, the nascent prairie strips consisted primarily of agricultural weeds and oats, with some prairie species in seedling stages. A multi-year study of ground dwelling arthropod communities (initially focused on Formicidae) was initiated in 2019 to examine the potential effects of prairie strip establishment and maturation (Helms et al. 2021). For this study we utilized data from the first year of this long-term effort, immediately after the strips were seeded. Like Helms (2021), we anticipated that the newly establishing strips would have little impact on carabid communities in the first year, which are largely determined by the previously established overwintering forms (Raderschall et al. 2022) and tested for such effects as described below.

Sampling Carabid Activity-density and Diversity

The study by Clark et al. (1997) sampled carabids in all seven MCSE cropping system treatments for a total of 42 plots and collected a total of 23,181 individuals (Clark et al. 1997). Their study utilized five pitfall traps per replicate (7 cm diameter with funnel) which were collected weekly. In 1994 (a soybean year), samples were collected from 5 July – 8 August; in 1995 (a wheat year), samples were collected from 22 May – 31 July. Due to the addition of the prairie strips, the sampling design in 2019 differed in several respects. In each plot, three transects were created running perpendicular from the prairie strip into the row crop. Transects were placed no closer than 10 m apart and terminated no closer than 20 m from a crop edge to control for edge effects. Along each transect, four sampling stations were established at distances of 0 (center of the prairie strip), 1, 5, and 20 m into the cropped area (Figure 2.1). Sampling

periods occurred five times throughout the growing season, roughly every month (May-September). To avoid over-sampling any specific area of a plot, the sampled transects were rotated weekly, i.e., a different transect was selected to be sampled each week with no sampling occurring during the fourth week of each sampling period. In 2019, there were 15 sampling weeks over the growing season from 13 May-19 September. To reduce disturbance in the plots, permanent sampling stations were established. At each station a 10 cm long by 5.8 cm (inside diameter) PVC pipe was buried into the soil and capped flush with the soil level. When utilized, the cap was removed, and a 5.8 cm diameter pitfall trap cup was placed into each PVC socket. Cups were filled with 60 ml of 95% ethanol and a drop of unscented dish soap to break surface tension. Pitfall traps were placed in the ground even with the surface and clear plastic covers were placed above each pitfall trap to protect from rainfall. Cups were collected after 48 h; on particularly hot, dry days, the ethanol was replenished after 24 h. All samples were sorted removing the Formicidae, and the remaining catch was placed in vials with 95% ethanol for storage (Helms et al. 2021). We subsequently sorted the samples, removing the carabids which were pinned and then identified to species using Lindroth (1961-1969), and verified by Dr. Gary Parsons, a Coleoptera specialist at Michigan State University.

Calculations for Comparison to Clark et al. (1997)

Carabid beetle captures were notably reduced in 2019 compared to 1994-95 and we wished to determine the extent of change in activity-density. We contacted the authors of Clark et al. (1997) for the original data, but it was not available, so our comparison is limited to data from figures and tables in the published paper. CMF and DAL independently extracted carabid activity-density metrics from the published figures using the on-line tool *PlotDigitizer.com* and compared the counts for accuracy. To adjust for differences in sampling design and duration between the two studies, we standardized comparisons by calculating the number of beetles caught per trap per day (Saska et al. 2022) over the same sampling period each year. The daily catch rate was calculated by dividing the total catch by the total sampling effort (number of traps per replicate x number of replicates x number of treatments x number of days each trap was deployed).

Clark et al. (1997) only reported the activity-density of the four numerically dominant species, i.e. the most abundant species collected during both years which made up 87% of all individuals captured. Other less abundant species were reported as a percentage of the overall

two-year catch across all treatments but were not specified at the treatment level and thus could not be directly contrasted to the 2019 data which focuses only on the Reduced Input and Biologically Based treatments. Therefore, we estimated changes in overall activity-density by assuming that the four dominant species in 1994-95 represented the entire community (i.e. as if no other species were captured) and compared the daily catch rates for those four species to the same time periods in 2019 with all species included. This provides the most conservative estimate of the reduction in total abundance over 25 years, with recognition that if the (unknown) number of additional beetles were added to the 1994-95 counts the magnitude of change would be larger. Next, to assess potential turnover in dominant species, we compared the catch rates of the four dominant species in 1994-95 to those for the same species in 2019. Since the sampling dates for 1994-95 in Clark et al. (1997) vary in crop type and emergence times for carabids, we also compared the daily catch rates in 2019 to each year individually (i.e., within the corresponding sampling dates for 1994 and 1995 separately) (Figure 2.4).

We did not adjust daily catch rates to account for differences in trap diameter (5.8 cm in 2019 vs. 7 cm in 1994-95) because while increased pitfall trap diameter can influence community composition of carabid catches by slightly favoring larger species it does not strongly impact estimates of activity-density (Luff 1975). To determine if observed changes in species turnover were potentially due to sampling bias, we measured the percent coverage (C) of the 2019 species diversity (Chao and Jost 2012).

Statistical Analysis for 2019 Community Comparisons

The 2019 dataset encompassed 720 48-hour trapping events (2 treatments x 6 replicates x 5 months x 3 transects x 4 distances from newly-establishing prairie strips). Since prairie strips were seeded just before data collection and not of primary interest for this study, we first tested whether distance from nascent strips (0, 1, 5, or 20 m) impacted carabid communities and found no evidence that this was the case (Table 2.2). Next, we tested for differences in activity-density between treatments and across months, pooling the catch from the 12 trapping events that occurred per replicate each month within each treatment. Using the R package *lme4* (Bates et al. 2015), we used Generalized Linear Mixed Models (GLMMs) with a Poisson distribution to test whether carabid activity-density differed by treatment (Reduced Input vs. Biologically Based), month (May - September), or their interaction (Table 2.3). We compared this model to its subsets based on QAICc. We then tested whether diversity differed between treatments. Diversity was

quantified three ways: as species richness, Hill-Shannon diversity (Jost 2006; see also Roswell et al. 2021), and Chao1 richness estimator (Chao and Chiu 2016). In all cases we summed the community across months to produce a single diversity estimate per replicate per treatment ($n = 6$), as diversity during any given month was low and considering months individually could hide effects of temporal turnover in composition. We used Linear Mixed models to test if diversity differed between treatments, with replicate as a random effect since the MCSE uses a randomized complete block design. Models for Hill-Shannon and Chao1 produced singular fits, so they were re-run as linear models with the random effect dropped. Post-hoc pairwise tests were performed using the “emmeans” function in the R package *emmeans* (Lenth et al. 2023) to determine significant pairwise differences within the best fit model. Finally, we used Permutational Multivariate Analysis of Variance (PERMANOVA) to test if community composition differed by treatment and/or month (Bray-Curtis dissimilarity, 999 permutations), using the *adonis2* function in the R package *vegan* (Oksanen et al. 2022). We used Non-metric Multidimensional Scaling (NMDS) to visualize these community differences (Bray-Curtis dissimilarity, $k = 3$, stress = 0.08). As in the previous analyses, for both the PERMANOVA and NMDS we pooled observations across months to compare the season-long communities per replicate field within each treatment.

RESULTS

Comparison to Clark et al. (1997)

In 1994-95, the numerically dominant species were *Cyclotrachelus sodalis* (LeConte), *Poecilus lucublandus* (Say), *Pterostichus melanarius* (Illiger), and *Agonum placidum* (Say); which made up 87% of the total capture across all seven treatments (Clark et al. 1997). In total, 7,470 individuals of these species were collected in the Reduced Input and Biologically Based treatments in 1994-95. In contrast, only 412 individuals of all carabid species were captured in the same treatments in the same time periods in 2019 (Table 2.6). After adjusting for sampling effort, the daily catch rates for all species captured in both treatments in 2019 were 58 - 76% lower than the same time periods in 1994 and 1995. Reduced catch rates in 2019 occurred across both treatments and for all four of the 1994-95 numerically dominant species (Figure 2.6). Overall, the activity-density of these four species declined between 94 - 98% over the 25-year period. Additional comparisons by individual species, treatment, and year can be found in Table 2.4.

We also observed a shift in the trophic position of the dominant species between the two studies. The most abundant species in Clark's study were predators, whereas in 2019 we found granivorous, and omnivorous species were dominant, specifically within the Biologically Based treatment. For example, predaceous *C. sodalis* and *P. lucublandus* were the two most abundant species in 1994-95 but both were rare in 2019 and replaced by the predators *Poecilus chalcites* (Say) and *Cicindelidia punctulata* (Olivier) (Table 2.7). In contrast, the granivorous *Harpalus compar* (LeConte) and *Harpalus pensylvanicus* (DeGeer) were the most abundant species in 2019, comprising nearly 45% of the total capture; but were rare in 1994-95 with *H. pensylvanicus* making up 3% of all captures (across all treatments in the array) and *H. compar* being either absent or making up such a small percent of the catch that it was not reported (Clark et al. 1997; Table 2.7).

Carabid Activity-density and Diversity

During the 2019 study, we collected 456 individual carabids, representing 34 species, during 720 total trapping events between 18 May-17 September 2019 (Table 2.7). We captured more than twice as many individuals in the Biologically Based treatment than in Reduced Input (321 vs. 135; Tables 2.7, 2.8). Differences in activity-density were due primarily to a few numerically dominant species in the Biologically Based treatment (Figure 2.2), particularly *H. compar* and *H. pensylvanicus*. Activity-density peaked in July and August and was significantly different compared to both early and late season across both treatments ($p < 0.001$) (Figure 2.5).

Community structure also differed between the treatments. While species richness was comparable between treatments, the Biologically Based community was less even, resulting in lower Hill-Shannon diversity (Table 2.8, Figure 2.6). We calculated Chao1 estimators for both treatments and found a greater expected species richness in Biologically Based. The Reduced Input treatment had 23 species and five singletons while the Biologically Based treatment had 29 species including 11 singletons (Table 2.8). Coverage estimates suggest we sampled 98% of the expected species richness across the two treatments; by treatment, we sampled 94% in Reduced Input and 97% in Biologically Based (Table 2.8). Finally, we compared the overall community composition of both treatments visually using a NMDS (Figure 2.7) coupled with a PERMANOVA test and determined the communities were significantly different ($F_{0,1} = 5.1141$, $p < 0.005$).

DISCUSSION

We found a shift in the activity-density and community composition of carabids at the KBS-LTER between 1994-95 and 2019. Specifically, we found evidence for a decline in the overall activity-density of carabids of 58-76% at a minimum and a 94-98% decline in the daily catch rate of the previously dominant species. Moreover, we found that community structural differences between treatments increased, resulting from loss of predatory species and increased dominance of granivores in 2019 compared to 1994-95.

Comparison to Clark et al. (1997)

The first objective of this study was to compare our findings for carabid community composition and activity-density to a 1994-95 study at the same site (Clark et al. 1997). We found that the overall activity-density of all carabids, and that of the formerly numerically dominant carabid species had declined precipitously (Table 2.4, Figure 2.4). Most notably, we found a severe decline in the activity-density of *C. sodalis* and *P. lucublandus*, which decreased from 31% and 25% of the total catch respectively in 1994-95 to less than 2% each in the combined treatments for 2019. An autumn breeder that overwinters in the larval form, *C. sodalis* is often cited in the literature as sensitive to disturbance and favors semi-natural grasslands (Larsen et al. 2003). The loss of *C. sodalis* in both cropping system treatments suggests the species is sensitive to long-term disturbance regimes caused by tillage, seeding, or harvesting of the row crop. Although Clark et al. (1997) found that *A. placidum* and *P. lucublandus* favored tilled croplands in the MCSE in 1994-95, they were largely absent by 2019 at which time the dominant predator was *P. chalcites*, which is known to be better adapted to managed landscapes (Larsen et al. 2003; Gardiner et al. 2010). Surprisingly, the invasive predator *P. melanarius* was not common in either of the treatments in 2019, despite a higher activity-density in 1994-95 and documented reports of high abundance across agroecosystems in the Midwest, US (Lindroth 1961-1969; Larsen et al. 2003).

Carabid Activity-density and Community Composition in 2019

After 25 years of consistent crop management, the carabid communities at KBS-LTER were dominated by either generalist predators or granivores depending on cropping treatment. The Reduced Input treatment, which receives agrochemical (herbicide and insecticide) applications and less tillage, is dominated by predaceous carabids. In comparison, the Biologically Based treatment, which receives zero input of agrochemicals but increased soil

disturbance to control weeds, is dominated by granivorous carabids, such as *H. compar* and *H. pensylvanicus*. We suspect some of these changes are the result of changes in food availability. Without herbicides, Foxtail species (*Setaria spp*), are difficult to control in the Biologically Based treatment (KBS-LTER Agronomy Data, field observations) and could be supporting the populations of the granivorous species *H. compar* and *H. pensylvanicus*. Kirk (1973) reported increased activity-density of *H. pensylvanicus* where foxtail was abundant. In the Biologically Based treatment, *H. compar* and *H. pensylvanicus* accounted for 60% of the total catch, whereas in the Reduced Input treatment these species were rarer, and the most common species was the predaceous beetle *P. chalcites* (which was relatively common across both treatments). The dominant species in 2019 are generalists with greater tolerance for disturbed environments. The results of our study further support that long-term, consistent crop management has led to distinct communities by treatment, despite crop rotation or variations in annual conditions.

Overall, we found a noticeable decline in the activity-density of carabids in 2019 relative to 1994-95 across both treatments. The change we documented is of a similar magnitude to declines in insect biomass found in long-term datasets in Europe, such as the 75% decline in flying insects observed by Hallman et al. (2017). A 44-year comparison experiment by Harris et al. (2019) at the Hubbard Brook Experimental Forest also found dramatic reductions in carabid capture rates. Like Harris, we argue that our observed change in carabid abundance is outside the natural range of variation in insect populations and indicative of larger population decline. As indicator species for ground-dwelling arthropods in managed landscapes, our findings on the impacts to carabids are relevant for future study and conservation of other service-providing arthropods within agricultural settings. However, it should be noted that unlike other long-term studies, we do not have continuous data from 1994-95 to 2019 and cannot assess trends beyond comparing the two time points.

Factors Affecting Carabid Community Composition

Multiple factors may be contributing to the species turnover and a decline in overall activity-density within the carabid community at the KBS-LTER site, including changes in abiotic factors, prey availability, and pesticide use that directly or indirectly influence carabids and their food sources.

Abiotic Conditions

Weather data for KBS-LTER suggests an increase in annual temperature and

precipitation events since 1989 (<https://lter.kbs.msu.edu/datatables/12>). Although emergence times and overall fitness for carabids may potentially be impacted by climate change (Pozsgai and Littlewood 2014), we did not find phenological changes in the dominant community over 25 years at the MCSE that could contribute to species turnover. The shift in community composition from 1994-95 to 2019 is more likely due to the long-term agricultural management strategies that either directly or indirectly impact carabids through reduced food availability or application of agrochemicals for pest and weed seed suppression.

However, it should be noted that Pozsgai and Littlewood (2014) suggest that carabid foraging, reproduction, and dispersal are vulnerable to variable spring weather and shortened summer seasons due to high temperatures and reduced soil moisture. According to the National Climate Assessment, precipitation in the Midwest is expected to increase 8-20% (although the consistency of precipitation events like flood or drought are difficult to predict) and temperature extremes will include 10 more days above 95 degrees Fahrenheit annually (USGCRP 2023).

Reduction in Prey Availability

Predatory ground beetles consume many agricultural pests (Lindroth 1961-1969; Douglas et al. 2015), and introduction of new insecticides and weed control methods could contribute to a loss of available prey. For example, the formerly abundant pest European corn borer (*Ostrinia nubilalis* (Huber)) (Hurley et al. 2002) and Western corn rootworm (*Diabrotica virgifera virgifera* (LeConte)) (Gassmann 2021) are now nearly completely controlled by Bt crop traits. Similarly, the soybean aphid (*Aphis glycines* (Matsumura)) is now suppressed by the widespread use of neonicotinoid seed treatments, although the effectiveness of seed treatment is debated (Gaspar et al. 2014). A long-term study at KBS-LTER on ladybeetles found declines in the populations of both native and exotic species, associated with the loss of their preferred prey, the soybean aphid; however, native ladybeetle populations tended to thrive in patches of refuge habitat with alternative prey (Bahlai et al. 2015). Furthermore, reduction in prey availability within the crop may encourage intraguild predation within carabids, or among predatory ground-dwelling arthropods. Not only will this influence overall carabid population activity-density and diversity, but also their pest suppression potential in crops.

Direct or Indirect Effects of Pesticides

Pesticides commonly used in Midwestern row crops could have both direct and indirect effects on carabids. Studies on the non-target impact of neonicotinoid seed treatments and other

synthetic insecticides have shown that ground dwelling arthropods, as natural predators and scavengers, are vulnerable to direct exposure and indirect loss of prey. A laboratory study of neonicotinoid treated seed by Mullin et al. (2005), resulted in near 100% mortality in 17 of the 18 species of carabids tested. Of those, *P. chalcites* and *H. pensylvanicus*, two of the numerically dominant species in our study, were noted as the most tolerant of both fungicide and neonicotinoid exposure and may have come to dominate the 2019 community in part for this reason.

Indirect exposure to insecticides, either through ingestion of exposed prey or prey that has fallen after a foliar application, is a likely pathway for non-target effects on carabids. In a study by Douglas et al. (2015) on the grey garden slug (*Deroceras reticulatum* (Müller)), an agricultural pest in soybean crops, the slugs were not affected by ingestion of neonicotinoid coated seeds; however, over 80% of the carabids that consumed the exposed slugs experienced some adverse effect. However, the chronic, non-target impacts of neonicotinoids on carabids are understudied. In our study, we found a prevalence of granivorous *Harpalus spp.* and the predator *P. chalcites* in both treatments at higher activity-density than either year of Clark et al. (1997). It may be possible that these species are more tolerant to insecticide use as compared to the numerically dominant species of 1994-95. In general, the literature suggests that long-term pesticide use and consistent disturbance from agricultural management practices are the primary cause of carabid declines in agroecosystems (Mullin et al. 2005; Douglas et al. 2015).

CONCLUSION

Impacts of long-term cropping system management are important in defining the community composition and activity-density of carabids in agroecosystems. When compared to a similar study on carabids 25 years prior at the KBS-LTER, we found a decline in overall activity-density and strong turnover in which species dominated the community. Our study found a distinct granivore-dominated community of carabids in the Biologically Based treatment that differed strongly from the Reduced Input treatment. This change could have been a result of multiple factors, including direct or indirect toxicity due to insecticide use, reduction in prey availability from the widespread use of seed treatments and Bt traits, competition, impacts of weed management, or changes in rainfall and temperature patterns due to climate change. This study demonstrates that even conservation-oriented practices can fail to halt insect decline and species turnover in agriculture. Future work must focus on functional implications of turnover in

carabid species composition in annual cropping systems, and on understanding the specific mechanisms that lead to these types of changes.

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APPENDIX. CHAPTER TWO FIGURES AND TABLES

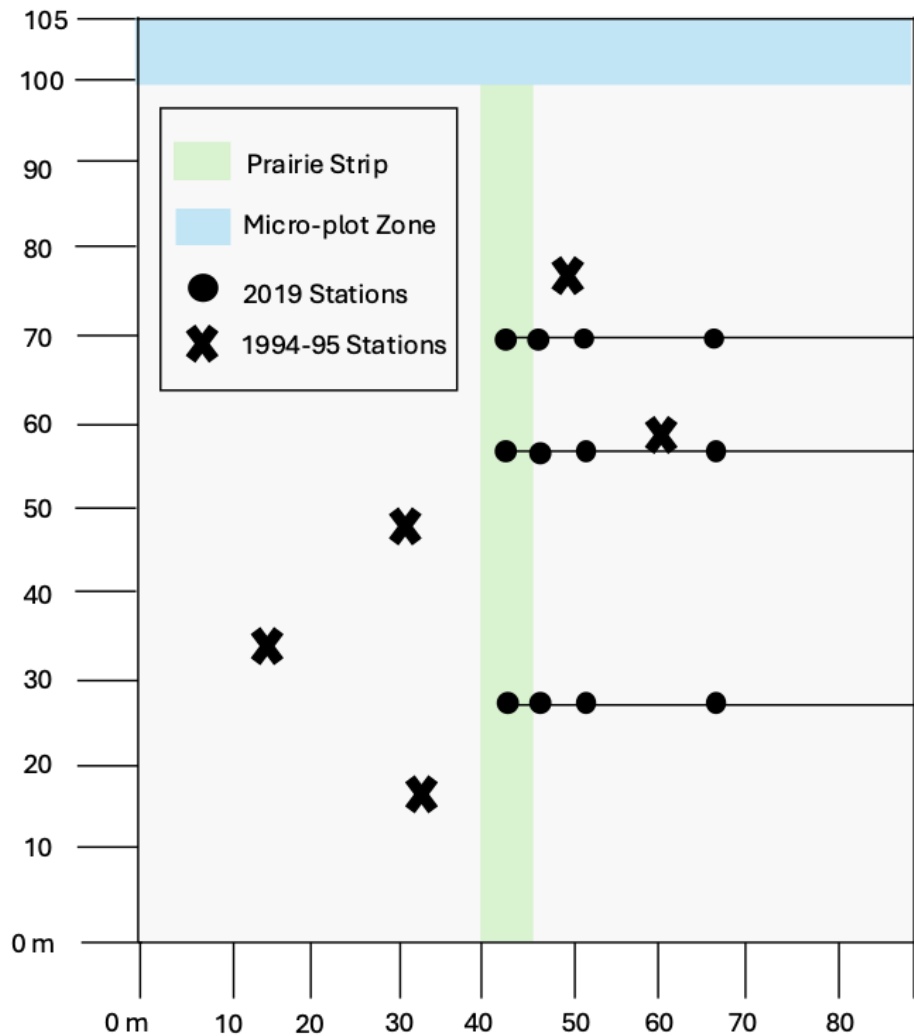


Figure 2.1. Experimental design for 2019 pitfall trap sampling showing three transects (North, Central, South) and sampling stations placed at varying distances from prairie strip (0, 1, 5, and 20m), and the five 1994-95 sampling stations for the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

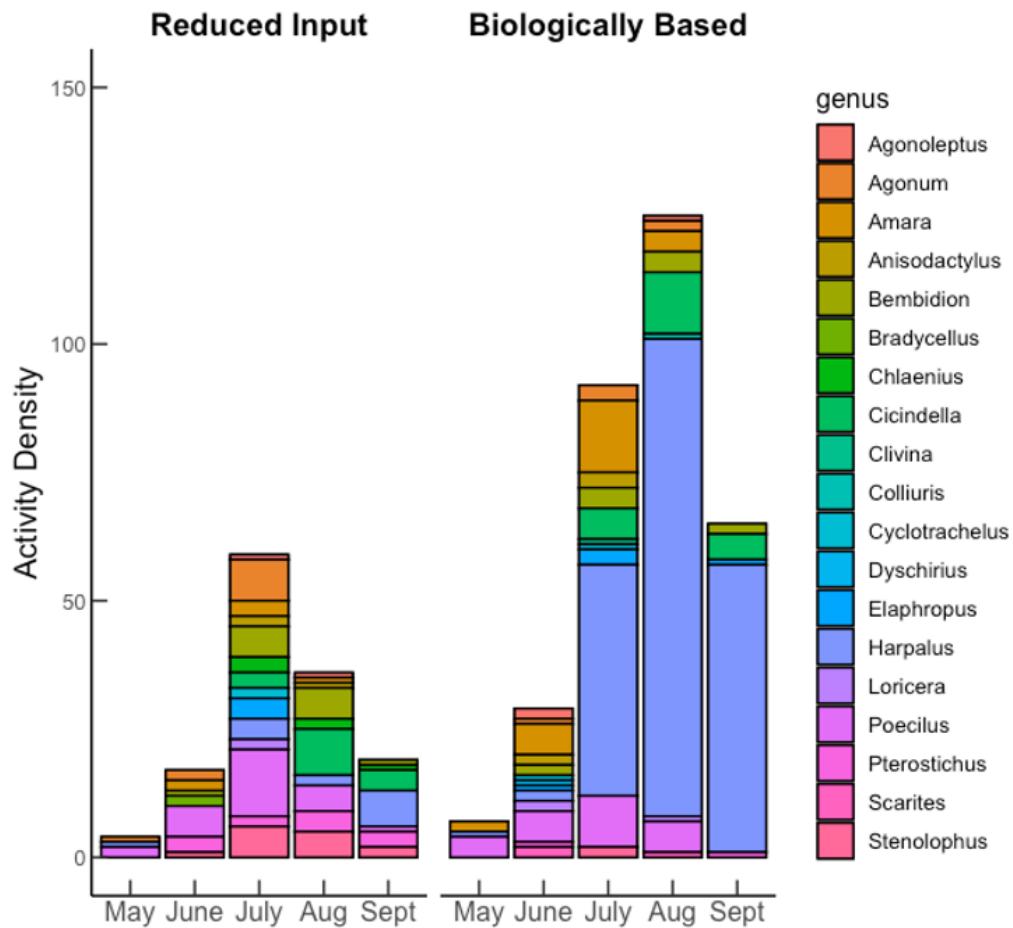


Figure 2.2. Comparison of activity-density by month and treatment. Activity-density (overall abundance) of 2019 carabids (visualized here by genus) was higher in the Biologically Based treatment as compared to Reduced Input at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Table 2.1 Details for agrochemical (fertilizer and pesticide) applications in 2018-2019 in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. See herbicide (<https://lter.kbs.msu.edu/datatables/160>), fertilizer (<https://lter.kbs.msu.edu/datatables/159>), and insecticide applications (<https://lter.kbs.msu.edu/datatables/161>) on the lter.kbs.msu.edu website.

Year	Treatment	Herbicide	Insecticide	Fertilizer
2018	Reduced Input	Herbicide Roundup Power Max (glyphosate 48.7%)	None	Fertilizer 0-0-60 potash fertilizer Ammonium sulfate (AMS)
2018	Biologically Based	None	None	
2019	Reduced Input	Herbicide PowerFlex HL Herbicide Roundup Power Max (glyphosate 48.7%)	None	Fertilizer 28% UAN (28-0-0) Sulfur (0-0-0-85) Fertilizer 0-46-0 phosphate fertilizer Fertilizer 0-0-60 potash fertilizer Ammonium sulfate (AMS) Custom mix Fertilizer 28% UAN (28-0-0) Custom mix
2019	Biologically Based	None	None	

Description of methods used for activity-density sampling in 2019 and removal of distance effects. For analyses presented in the main text we pooled our catch across all trapping events within a replicate, either broken down by month (for abundance) or with all observations compiled across the season (for diversity). This occurred because our primary goal was to characterize community differences between the two cropping system treatments, and because the catch rate was generally low (mean 0.68 beetles per trap). However, traps were situated at different distances from newly-established prairie strips in all replicates that were seeded the same year as data were collected, at 0, 1, 5, or 20 m from the strip. To test for effects of distance from prairie strips we constructed a generalized linear mixed effects model (negative binomial distribution) in the R package *lme4* in which we modeled carabid abundance as a function of distance from strips (main effect) and replicate (random effect). We compared this model to a null model without the main effect term using a likelihood ratio test. The model with a term for distance from strips failed to outperform the null model (Table S2), suggesting limited impact of distance from prairie strips on carabid abundance in 2019.

Table 2.2. Model comparison showing that distance from nascent prairie strips had limited effects on abundance for beetles collected in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Name	Model Test (Negative Binomial)	AIC	X ²	Df	P-value
Null	abundance ~ (1 rep)	894.43		-	-
Distance	abundance ~ distance + (1 rep)	89832	2.12	3	0.55

Table 2.3. Model comparison table showing best fit model for carabid abundance (Poisson GLMM) beetles collected in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Model Test (Poisson GLMM): abundance ~ treatment * month + (1 rep)					
Variable					
Month	Treatment	Interaction	df	QAICc	Weight
+	+		7	184.8	0.91
+	+	+	11	189.3	0.1
+			6	221.8	0
	+		3	288.5	0
			2	325.9	0

Table 2.4. The four numerically dominant carabid species (Clark et al. 1997) in A) 1994 had higher daily catch rates (standardized catch/trap/day) compared to the same species in B) 2019 in a similar timeframe. The daily catch rates in C) 1995 also had higher daily catch rates compared to the same species in D) 2019 in a similar timeframe for both the Reduced Input and Biologically Based treatments. Percent decline in A)1994 and B)1995 as compared to 2019 suggest a ~96% decline in numerically dominant carabid species at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

A)							
Clark et al. 1994 (5 July – 8 August)							
Species	Reduced Input	c/t/d	Biologically Based	c/t/d	Total	c/t/d	
<i>Cyclotrachelus sodalis</i> (LeConte)	252	0.24	348	0.33	600	0.29	
<i>Poecilus lucublandus</i> (Say)	450	0.43	546	0.52	996	0.47	
<i>Pterostichus melanarius</i> (Illiger)	768	0.73	552	0.53	1320	0.63	
<i>Agonum placidum</i> (Say)	132	0.13	288	0.27	420	0.20	
Total	1602	1.53	1734	1.65	3336	1.59	
B)							
2019 (8 July – 7 August)							
Species	Reduced Input	c/t/d	Biologically Based	c/t/d	Total	c/t/d	% Decline
<i>Cyclotrachelus sodalis</i> (LeConte)	2	0.01	1	0.01	3	0.01	97.27
<i>Poecilus lucublandus</i> (Say)	2	0.01	0	0	2	0.01	98.90
<i>Pterostichus melanarius</i> (Illiger)	3	0.02	0	0	3	0.01	98.76
<i>Agonum placidum</i> (Say)	7	0.04	4	0.02	11	0.03	85.68
Total	14	0.07	5	0.03	19	0.05	96.89
C)							
Clark et al. 1995 (22 May – 31 July)							
Species	Reduced Input	c/t/d	Biologically Based	c/t/d	Total	c/t/d	
<i>Cyclotrachelus sodalis</i> (LeConte)	264	0.12	264	0.12	528	0.12	
<i>Poecilus lucublandus</i> (Say)	1092	0.51	840	0.39	1932	0.45	
<i>Pterostichus melanarius</i> (Illiger)	216	0.10	240	0.11	456	0.11	
<i>Agonum placidum</i> (Say)	522	0.25	696	0.33	1218	0.29	
Total	2094	0.98	2040	0.96	4134	0.97	
D)							
2019 (21 May – 25 July)							
Species	Reduced Input	c/t/d	Biologically Based	c/t/d	Total	c/t/d	% Decline
<i>Cyclotrachelus sodalis</i> (LeConte)	2	0.01	2	0.01	4	0.01	95.80
<i>Poecilus lucublandus</i> (Say)	3	0.01	0	0	3	0.01	99.14
<i>Pterostichus melanarius</i> (Illiger)	5	0.02	1	0.003	6	0.01	92.70
<i>Agonum placidum</i> (Say)	9	0.03	4	0.01	13	0.02	94.08
Total	19	0.06	7	0.02	26	0.039	96.51

Table 2.5. Calculation of total sampling effort for carabids in 1994-95 and 2019. Due to different time frames in Clark et al. (1997), the 2019 sampling effort is displayed as 2019 (a) to compare 1994 sampling dates, and 2019 (b) to compare 1995 sampling dates. The final daily catch rates are calculated by dividing the total activity-density (abundance) of carabids during that sample period by the total sampling effort.

Year	Days	Treatment	Replicate	Active Traps	Total Effort
1994	35	1	6	5	1050
1994	35	2	6	5	2100
1995	71	1	6	5	2130
1995	71	2	6	5	4260
2019 (a)	8	1	6	4	192
2019 (a)	8	2	6	4	384
2019 (b)	14	1	6	4	336
2019 (b)	14	2	6	4	672



Figure 2.3. Experimental design for the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI (Robertson and Hamilton 2015).

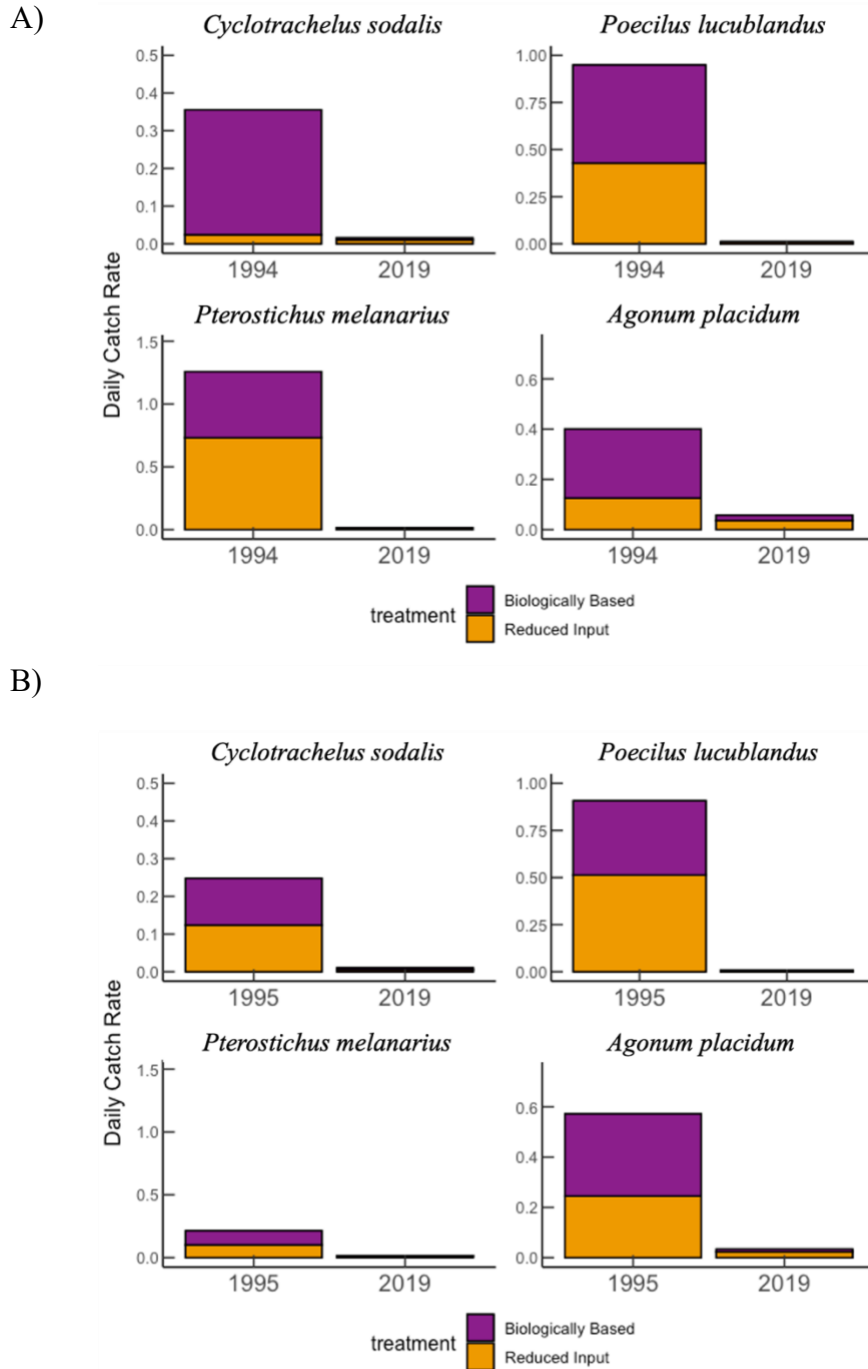


Figure 2.4. Daily catch rates for the dominant carabid species in A)1994 and B)1995 as compared to 2019. The four numerically-dominant carabid species in 1994-95 (22 May – 8 August; Clark et al. 1997) had higher daily catch rates compared to 2019 (21 May – 7 August) for both the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

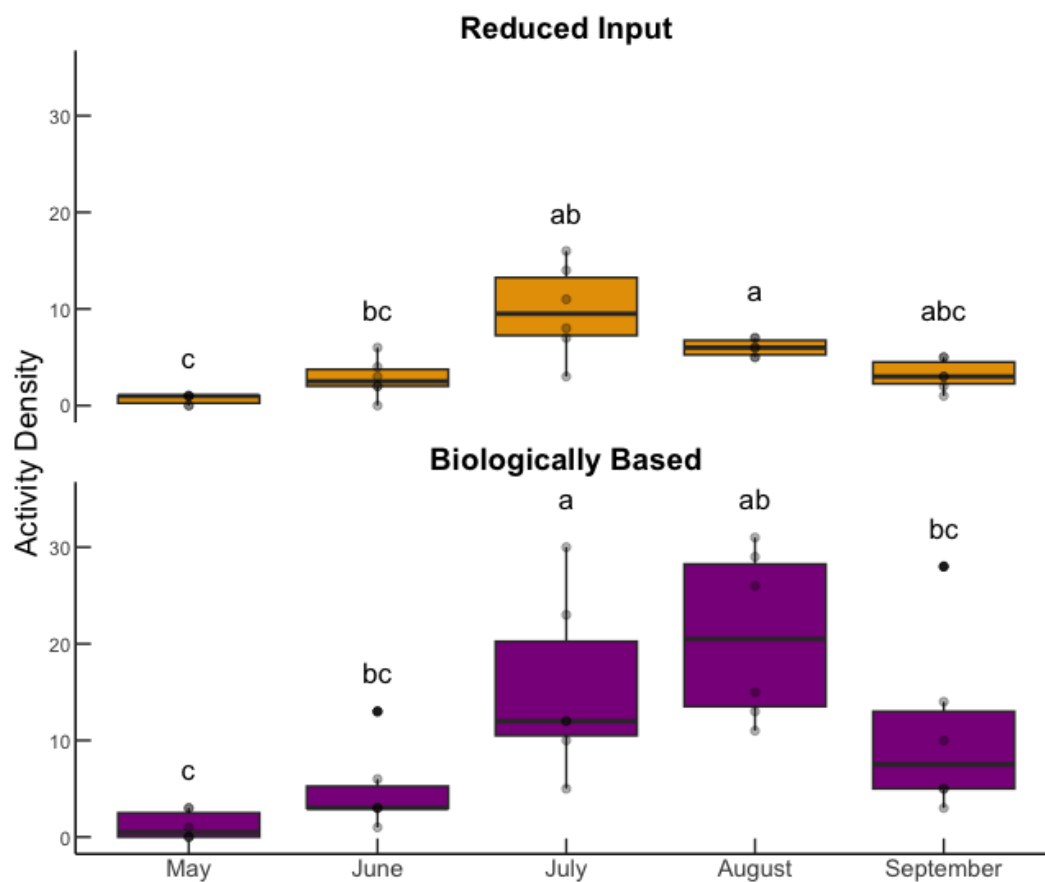


Figure 2.5. Comparison of activity-density (abundance) for 2019 by month and treatment. Activity-density per plot in 2019 was higher in the Biologically Based treatment than Reduced Input and peaked during July and August, respectively. By treatment, early and late season were significant compared to mid-season activity-density. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

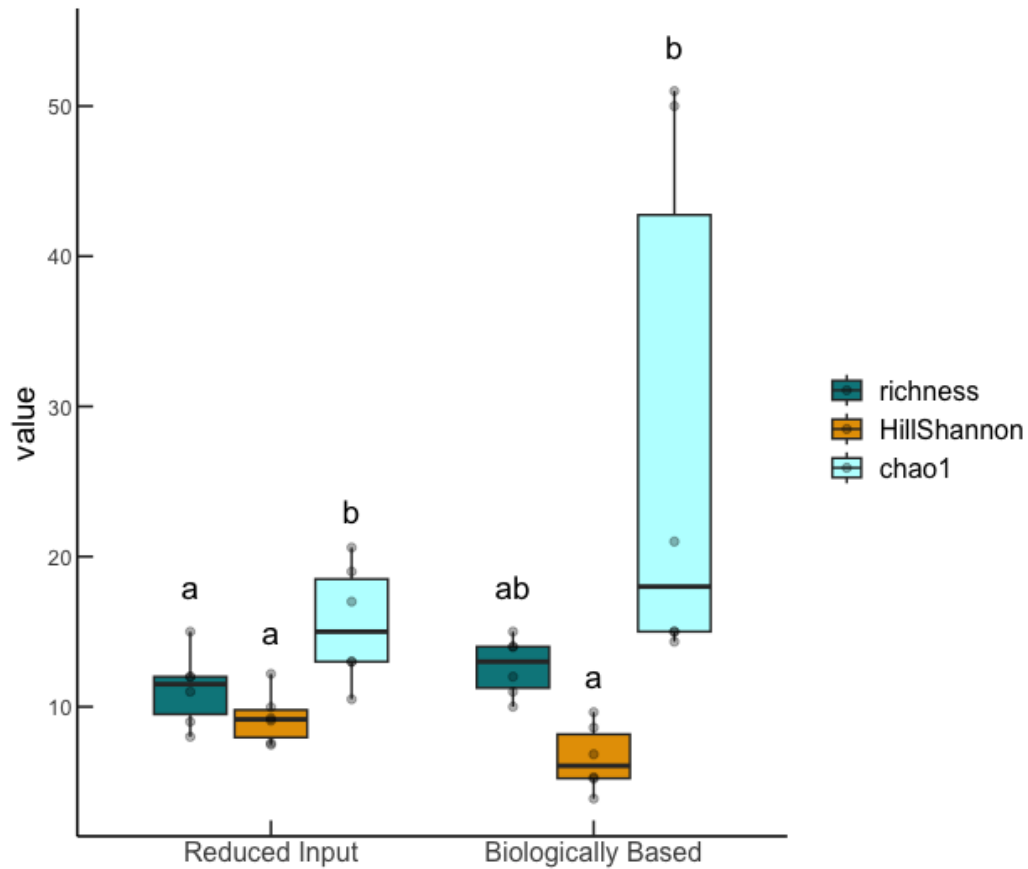


Figure 2.6. Comparison of diversity metrics (richness, Shannon Hill, and chao1 estimate) for 2019 by treatment. Diversity metrics for 2019 carabid species was similar for both richness and Hill-Shannon adjusted richness, but varied for chao1 diversity estimate in the Biologically Based treatment compared to Reduced Input, within the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI

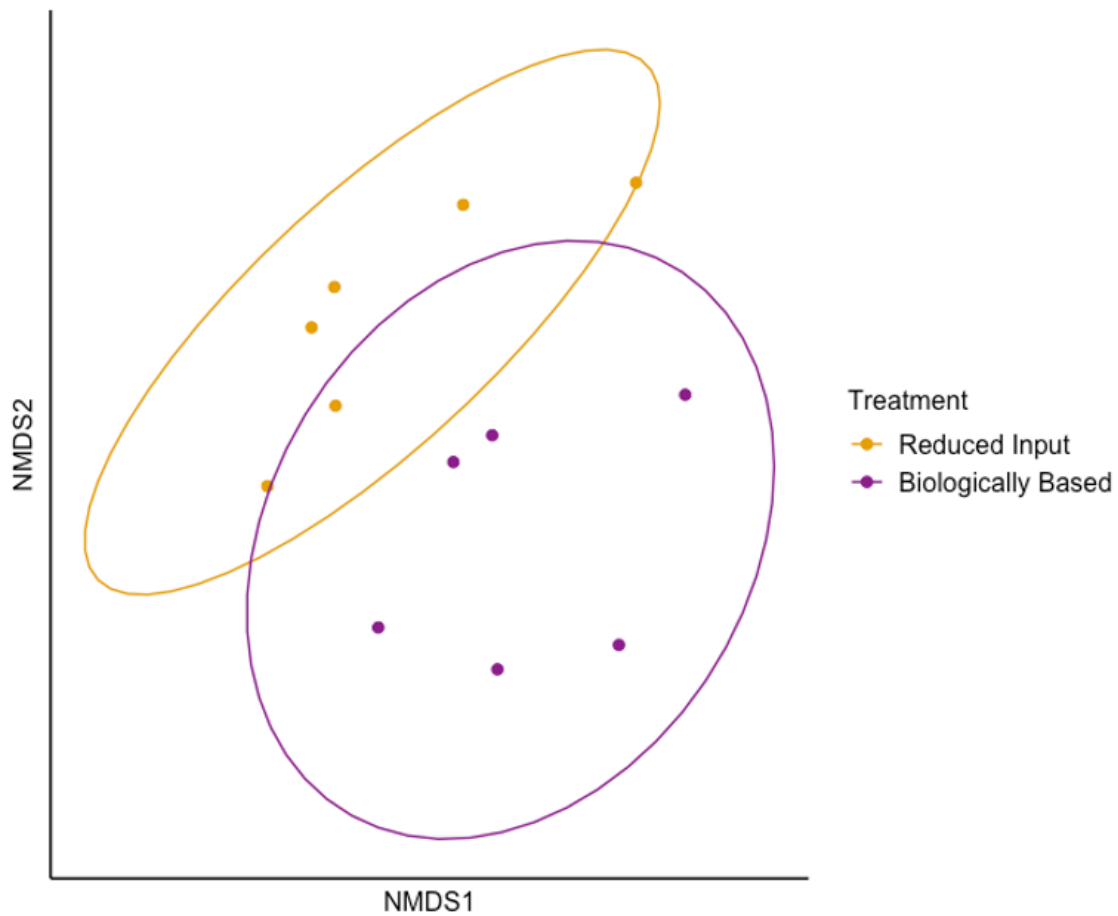


Figure 2.7. Non-metric Multidimensional Scaling (NMDS) graphical comparison of 2019 carabid community composition by treatment. The NMDS plot (Bray-Curtis dissimilarity, $k = 3$, stress = 0.08) illustrates that community composition differs between Reduced Input and Biologically Based treatments within the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Table 2.6. Minimum estimated percent decline in carabid activity-density from 1994-95 to 2019 in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. Due to the way data were reported in Clark et al. (1997), this table contrasts the daily catch rate for the four numerically dominant species in 1994-95 to all species captured in 2019. Thus, this is a conservative estimate of the actual community wide decline in activity-density.

Treatment	1994-95 Daily Catch Rate per Trap	2019 Total Catch	1994-95 Total Catch	2019 Daily Catch Rate per Trap	Minimum % Decline
1994 Reduced Input	1.53	71	267	0.37	-75.82
1994 Biologically Based	1.65	133	289	0.69	-58.18
1995 Reduced Input	0.98	79	349	0.24	-75.51
1995 Biologically Based	0.96	129	340	0.38	-60.42

Table 2.7. Summary of 2019 carabids by total count, percent, and rarity (<1% of total) by treatment (Reduced Input and Biologically Based) and overall, at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Species	Reduced Input				Biologically Based			Total (all treatments)		
	Function	Count	%	Rare <1%	Count	%	Rare <1%	Count	%	Rare <1%
<i>Agonoleptus conjunctus</i> (Say)	Predator	2	1.48		3	0.93	R	5	1.10	
<i>Agonum cupripenne</i> (Say)	Predator	2	1.48		1	0.31	R	3	0.66	R
<i>Agonum octopunctatum</i> (Fabricius)	Predator	0	0		1	0.31	R	1	0.22	R
<i>Agonum placidum</i> (Say)	Predator/Omnivore	9	6.67		5	1.56		14	3.07	
<i>Amara familiaris</i> (Duftschmid)	Omnivore	2	1.48		15	4.67		17	3.73	
<i>Amara littoralis</i> (Mannerheim)	Omnivore	4	2.96		10	3.12		14	3.07	
<i>Amara pensylvanicus</i> (DeGeer)	Granivore/Omnivore	0	0		1	0.31	R	1	0.22	R
<i>Anisodactylus rusticus</i> (Say)	Omnivore	0	0		5	1.56		5	1.10	
<i>Anisodactylus sanctaecrucis</i> (Fabricius)	Omnivore	3	2.22		0	0.00		3	0.66	R
<i>Bembidion quadrimaculatum</i> (Linnaeus)	Predator	4	2.96		5	1.56		9	1.97	
<i>Bembidion rapidum</i> (LeConte)	Predator	0	0.00		2	0.62	R	2	0.44	R
<i>Bembidion versicolor</i> (LeConte)	Predator	10	7.41		5	1.56		15	3.29	
<i>Bradycellus ruprestis</i> (Say)	Predator	2	1.48		0	0		2	0.44	R
<i>Chlaenius tricolor</i> (Dejean)	Predator	6	4.44		0	0		6	1.32	
<i>Cicindela punctulata</i> (Olivier)	Predator	16	11.85		23	7.17		39	8.55	
<i>Clivina impressifrons</i> (LeConte)	Predator/Omnivore	0	0		1	0.31	R	1	0.22	R
<i>Colliuris pensylvanicus</i> (Linnaeus)	Predator	0	0		1	0.31	R	1	0.22	R
<i>Cyclotrachelus sodalis</i> (LeConte)	Predator/Omnivore	2	1.48		2	0.62	R	4	0.88	R
<i>Dyschirius truncatus</i> (LeConte)	Predator	0	0.00		1	0.31	R	1	0.22	R
<i>Elaphropus anceps</i> (LeConte)	Predator/Omnivore	4	2.96		5	1.56		9	1.97	
<i>Harpalus affinis</i> (Schränk)	Granivore/Omnivore	1	0.74	R	1	0.31	R	2	0.44	R
<i>Harpalus caliginosus</i> (Fabricius)	Granivore/Omnivore	0	0		2	0.62	R	2	0.44	R
<i>Harpalus compar</i> (LeConte)	Granivore/Omnivore	4	2.96		117	36.45		121	26.54	
<i>Harpalus herbivagus</i> (Say)	Granivore/Omnivore	1	0.74	R	1	0.31	R	2	0.44	R
<i>Harpalus pensylvanicus</i> (DeGeer)	Granivore/Omnivore	8	5.93		75	23.36		83	18.20	
<i>Harpalus rubripes</i> (Duftschmid)	Omnivore	0	0		3	0.93	R	3	0.66	R
<i>Loricera pilicornis</i> (Fabricius)	Predator	2	1.48		3	0.93	R	5	1.10	
<i>Poecilus chalcites</i> (Say)	Predator/Omnivore	24	17.78		26	8.10		50	10.96	
<i>Poecilus lucublandus</i> (Say)	Predator/Omnivore	3	2.22		0	0		3	0.66	R
<i>Pterostichus melanarius</i> (Illiger)	Predator	12	8.89		1	0.31	R	13	2.85	
<i>Pterostichus permundus</i> (Say)	Predator/Omnivore	0	0		1	0.31	R	1	0.22	R
<i>Scarites vicinus</i> (Chaudoir)	Predator	0	0		3	0.93	R	3	0.66	R
<i>Stenolophus ochropezus</i> (Say)	Predator/Omnivore	12	8.89		2	0.62	R	14	3.07	
<i>Stenolophus plebejus</i> (Dejean)	Predator	2	1.48		0	0		2	0.44	R
Total		135			321			456		

Table 2.8. Summary table for 2019 carabid diversity metrics by treatment (Reduced Input and Biologically Based) at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

Diversity Metrics	Reduced Input	Biologically Based	All Treatments
Total Count	135	321	456
Genus	15	17	19
Species	23	29	34
Singletons	5	11	6
Doubletons	7	10	6
Shannon Diversity (H')	2.77	2.16	2.56
Shannon Evenness (E)	0.88	0.64	0.73
Coverage % (C)	93.63	97.23	98.25

CHAPTER THREE: PERENNIAL PRAIRIE STRIPS INCREASE BIODIVERSITY OF GROUND BEETLES (COLEOPTERA: CARABIDAE) IN CONSERVATION- ORIENTED CROPPING SYSTEMS

ABSTRACT

Agricultural advancements have increased global food availability at the expense of ecosystem health and services. The simplification of agricultural landscapes has contributed to habitat loss and fragmentation, and thus global biodiversity loss. However, conservation interventions within agriculture have potential to reduce the ecological consequences of intensive practices and offer an option for a more sustainable food system. One such solution is prairie strips, or plantings of native, perennial forbs and grasses strategically established within agricultural fields to enhance ecosystem services. In 2019, prairie strips were planted in two conservation-oriented treatments at the Kellogg Biological Station (KBS) Long-term Ecological Research (LTER) site in Southwest Michigan. The treatments included Reduced Input which receives approximately one-third the conventional amount of synthetic chemical inputs, and Biologically Based which does not receive any synthetic inputs. Here, we studied the effects of prairie strip establishment on the community composition and diversity of ground beetles (Coleoptera: Carabidae) from 2019-2022. Carabids are beneficial predators within row crop agriculture and serve as useful indicators of agroecosystem sustainability. We found that prairie strips increased overall carabid activity-density and species turnover in ways strongly dependent on cropping treatment. The Biologically Based treatment harbored higher species richness, and increased carabid abundance one-year after prairie strip seeding. Across both treatments, we found 11 species that occurred only within the prairie strips, 6 species only within the crop field, and 18 species across both locations; further, we found 11 species were initially found only in the prairie strip in 2019 but by 2022 were found only in the crop field. Our study demonstrates that mature prairie strips harbor distinct communities and contribute to the spillover of biodiversity to adjacent row crops. As carabids are indicators for the response of ground-dwelling arthropod predators to agricultural management, farmers investing in conservation interventions may benefit from increased pest and weed suppression. Prairie strips offer one solution to meet global conservation goals, by introducing natural refuge into otherwise highly simplified landscapes to increase biodiversity and benefit farming communities.

INTRODUCTION

Over the last century, the intensification of agriculture has led to increased productivity but often at the expense of other ecosystem services. While advancements in technology have contributed to an increase in global average food availability (Smith et al. 2014), other critical ecosystem services in agriculture such as natural pest suppression (Rusch et al. 2016) and pollination (Kremen 2002) have declined, in parallel with an overall loss of biodiversity (Blitzer et al. 2012; Newbold et al. 2015; Wagner 2020). In addition, agricultural intensification can result in the simplification of arable landscapes (Tscharntke et al. 2005, 2012; Fahrig 2013) which may lack the ability to support biodiversity of plants, insects, and wildlife (Tilman et al. 2001; Martin et al. 2019; Iuliano 2024) and are unlikely to recover without intervention (Isbell et al. 2019).

Resilient agroecosystems depend on a diverse species pool to maintain diverse populations of multiple taxa across agricultural landscapes (Tscharntke et al. 2005; 2007). Non-crop habitats provide both an avenue for dispersal and refuge for birds, insects, and wildlife. Cropland expansion, however, has resulted in the loss of native refuge and the decline in both biodiversity and ecosystem services (Foley et al. 2005). Conservation interventions within agriculture have been shown to reduce negative ecological consequences of intensive practices and offer an option for a more sustainable food system. Termed “ecological intensification” (Tilman et al. 2014), multifunctional landscapes sustain crop yield through integrating ecosystem services that support food production (Kremen 2020), biodiversity conservation (Geertsema et al. 2016) and augment or replace fertilizer and pesticide inputs (Kleijn et al. 2019).

Midwestern US row crop agriculture has become highly simplified with a loss of biodiversity and ecosystem services (Liebman and Schulte 2015; Lark et al. 2020), but conservation practices have been developed to address this situation. The Conservation Reserve Program (CRP) of the US Farm Bill provides farmers and landowners technical and financial support to convert arable land to native habitats. Prairie strips are a novel CRP-eligible conservation practice with the potential to increase biodiversity and multiple ecosystem services (USDA 2025). Prairie strips are plantings of native, perennial forbs and grasses planted within agricultural fields to reduce soil erosion and water pollution (Helmets et al. 2012) but have proven to have other benefits. Researchers at Iowa State University created the Science-based Trials of Row-crops Integrated with Prairie Strips project (STRIPS) and strategically positioned

contour prairie strips in row crops to slow water movement, increase infiltration, and retain nutrients, with runoff of sediment, phosphorus, and nitrogen reduced by 1.6 times compared to fields without strips (Schulte et al. 2017). In addition, prairie strips have proven to enhance other ecosystem services, such as pollination, pest suppression, decomposition, or soil health (Kemmerling et al. 2022).

Prairie strips have been shown to enhance biodiversity harboring more birds (Schulte et al. 2016; Giese et al. 2024) more insect taxa overall, and greater numbers of pollinators and natural predators than fields without strips (Schulte et al. 2017). In Iowa, positive impacts on native bee diversity (Kordbach et al. 2020), and honeybee health and productivity have been documented (Zhang et al. 2023), while impacts on natural enemies and predation services are more variable (Cox et al. 2014; Vargas 2024). In Michigan, newly established prairie strips increased diversity of soil microbial communities (Rutkowski and Evans 2025), supported greater dung beetle abundance, spider abundance and richness (Kemmerling et al. 2022), and supported increased butterfly abundance (Kemmerling et al. 2023) than associated crop fields.

Perennial semi-natural land features (Holland et al. 2016), including field margins (Thomas et al. 2002), and managed beetle banks (MacLeod et al. 2004) provide habitat for ground-dwelling predators, and can enhance natural pest suppression within agroecosystems. Ground beetles (Coleoptera: Carabidae), or carabids, are beneficial predators within row crop agriculture and serve as useful indicators of biodiversity across agroecosystems (Makwela et al. 2023). Agricultural management practices such as soil fertilization and tillage, crop type, and pesticide application influence beetle fitness, community composition, and efficiency as service-providers (Kromp 1999). Carabids often benefit from perennial non-crop habitats within intensive row-crop agriculture that diversify the landscape and provide refuge from physical disturbance or pesticide use. Non-crop habitat also provide resources for overwintering and alternative prey not found in the crop field (Lee et al. 2001, Massaloux et al. 2020; Robinson et al. 2021). Prior studies have shown that carabids can rapidly colonize even nascent perennial habitats, increasing species diversity and abundance, and providing species spillover into adjacent crops (Lys and Nentwig 1994; Frank 1997, 1999). Given the similarity of prairie strips to other perennial habitat management practices with proven benefits to carabids, we hypothesized that prairie strips would have an impact on carabid communities in row crop settings. Specifically, we predicted that abundance and diversity of the carabid communities will

increase within the prairie strip but vary by cropping treatment due to legacy effects of long-term agricultural management (Fiser et al. 2025). We further predicted that prairie strips will increase spillover of carabid biodiversity and abundance into adjacent row crops.

METHODS AND MATERIALS

Study Site

This study took place from 2019-2022 at the Kellogg Biological Station (KBS), Long-term Ecological Research (LTER), Main Cropping System Experiment (MCSE) in Hickory Corners, Michigan (42.411078, -85.377195). The LTER MCSE was established in 1989 and consists of seven treatments along a gradient of agricultural management intensity including annual cropping systems, perennial cropping systems and a largely unmanaged early successional system (Robertson and Hamilton 2015). Treatments are arranged in a randomized complete block design of 0.88 ha plots (87 m x 105 m) replicated n=6 times (Figure 3.9). Annual crop treatments follow a corn (*Zea mays* L.) - soybean (*Glycine max* (L.) Merr.) - wheat (*Triticum aestivum* L.) rotation with corn and soybean planted in the spring and harvested in the fall and wheat planted late fall and harvested the following year (Robertson and Hamilton 2015).

The two treatments used in this study, Reduced Input and Biologically Based, are ‘conservation-oriented’ systems which differ from the conventional row crop management in the level of synthetic chemical inputs and the use of cover crops. Reduced Input uses one third the level of inputs used in conventional row crops, while Biologically Based does not receive synthetic inputs outside of occasional (ca. every 3 decades) fertilizer inputs used to offset crop removal. Reduced Input is managed for weeds with pre-emergence herbicides and both treatments are rotary-hoed and cultivated as necessary. Prior to seeding winter cover crops, both treatments are chisel-plowed and soil finished. Following corn, a cereal rye (*Secale cereale* L.) cover crop is planted, and following wheat red clover (*Trifolium pratense* L.) is planted. Agronomic management goals at the KBS-LTER have remained in place since 1989 with slight variations in application rates to reflect pest outbreaks, nutrient deficiencies, or adjust to current conventional practices (Table 3.10). Full management details can be found in the agronomic log available at the KBS-LTER website (kbs.lter.msu.edu).

Prairie Strips

On 25 April 2019, prairie strips were established in all replicates of the Reduced Input and Biologically Based treatments. The strips are 5 m wide x 105 m long and were placed in the

middle of each plot, dividing it in half lengthwise (Figure 3.10). The main objective for establishing the strips was to increase biodiversity of the annual crop systems to enhance pollination, pest suppression, and improve soil health. To achieve these objectives, a native perennial prairie seed mix was created including a mix of 4 warm- and cool-season grasses and 18 forb species (Table 3.11). Grasses were selected to provide a mix of cool and warm season species while forbs were selected to provide continuous floral resources over the entire growing season from May-October. In our region, perennial prairie plantings take six or more years to reach full maturity. Following best management practices, annual oat and rye (*Secale cereale* L.) nurse crops were added to the seed mix to suppress weeds in the establishment year. Prairie strips were also mowed several times during the first growing season to prevent annual weeds from setting seed and burned in subsequent springs to suppress woody vegetation. Full details can be found in the agronomic log available at the KBS-LTER website (kbs.lter.msu.edu).

Sampling for Carabid Diversity and Abundance

In this study, we examined the effects of prairie strip establishment on the community composition, activity-density (abundance), and within-treatment spatial distribution of ground beetles from 2019-2022. A primary research objective was to determine to what degree strips influence species ‘spillover’ into the adjacent row crop. To study this, three transects placed perpendicular to the prairie strip at 25, 55, and 70 m from the southern plot edge and extending 20 m from the strip into the surrounding row crop (Figure 3.10). To reduce edge effects, no sampling occurred within 20 m of any exterior plot edge. Permanent sampling stations were placed along each transect at 0 m (center of prairie strip) and 1, 5, and 20 m from the prairie strip edge. Pitfall traps were placed at each sampling station and consisted of a 5.8 cm wide plastic cup filled with ~60 ml of 95% ethanol and a drop of unscented dish soap to reduce surface tension. Each cup was placed in a 10 cm long x 5.8 cm wide (inside diameter) PVC tube dug into the soil with the rim even with the soil surface and capped when not in use. In addition, clear plastic rain guards were placed a few centimeters above each pitfall trap and secured with metal ground staples to reduce rainfall and soil entry.

As detailed in Helms et al. (2021), the individual transect sampled was rotated weekly during each sampling period to avoid oversampling local arthropod populations, with no sampling occurring during the fourth week. All sampling occurred from June- September 2019-2022. For each sampling period, pitfall traps were opened and then picked up in sequential order

after 48 hr and occasionally refilled with ethanol after 24 hr during hot, dry conditions. All samples were sorted to remove Formicidae for another study (Helms et al. 2021; Kemmerling et al. 2022) then filled with 95% ethanol and placed in storage. We subsequently sorted these samples removing carabids, which were pinned and identified to species (Lindroth 1961-1969).

Statistical Analysis for 2019-2022 Community Composition

In total, there were 2,304 48-hour trapping events for the 2019-2022 dataset (2 treatments x 6 replicates x 4 months x 3 transects x 4 sampling stations/transect x 4 years). To avoid bias when comparing species richness across years, we rarefied the samples to calculate the expected species richness based on individuals sampled using the R function “rarefy” in the *vegan* package (Oksanen et al. 2022). Furthermore, we used coverage estimates to test for total estimated biodiversity per year and treatment as represented by the total sampling efforts (Roswell et al. 2021).

We used the R package *lme4* (Bates et al. 2015) to test for differences in activity-density between treatments, year, season, and distance, by pooling the catch from the 12 trapping events that occurred per replicate each month, and within each treatment per year. We used Generalized Linear Mixed Models (GLMMs) with a negative binomial distribution to test multiple variables influencing carabid community dynamics including year (i.e. crop rotation), season (June-September), treatment (Reduced Input vs. Biologically Based), and distance from prairie strip (0, 1, 5, or 20 m) to test for differences and/or interactions with replicate as a random effect. We further tested for interactions between treatment*month, treatment*distance, and month*distance. We compared this model to its subsets based on QAICc. Post-hoc pairwise tests were performed using the “emmeans” function in the R package *emmeans* (Lenth et al. 2023) to determine significant pairwise differences within the best fit model. Finally, we used Permutational Multivariate Analysis of Variance (PERMANOVA) to test if community composition differed by treatment, month, and/or distance (Bray-Curtis dissimilarity, 999 permutations), using the “adonis2” function in the R package *vegan* (Oksanen et al. 2022). We used Non-metric Multidimensional Scaling (NMDS) to visualize these community differences (Bray-Curtis dissimilarity, k = 3, stress = 0.097). As in the previous analyses, for both the PERMANOVA and NMDS we pooled observations across months to compare the season-long communities per replicate field within each treatment.

To compare the prairie strip directly to the adjacent row crop, we applied both Hedge’s g

effect sizes and Sorenson's Dissimilarity to samples collected either within the prairie strip center (0 m) or at field center (20 m) by year and treatment. We determined the Hedge's g effect size using the *effectsize* package in R (Ben-Shachar et al. 2020), using the field center (20 m) as a baseline and comparing 0, 1, and 5 m from strip edge. We then used dissimilarity to compare the beta diversity or Nestedness and species turnover using the *betapart* package in R (Baselga et al. 2023).

Functional Diversity

Functional diversity metrics we considered for carabids included diet (predator, omnivore, or granivore), overwintering status (larval or adult), and flight ability (macropterous or brachypterous). Diet and flight abilities were determined through a literature search (Lindroth 1961-1969; Gardiner et al. 2010; www.bugguide.net).

RESULTS

Carabid Abundance and Community Composition

In total, 2,452 carabids representing 50 species and a variety of dietary, overwintering, and flight capabilities were collected across both treatments from 2019-2022 (Table 3.1). Notably, just two species *Harpalus compar* (LeConte) and *Harpalus pensylvanicus* (DeGeer) comprised 46.2% (2019) to 55.9% (2021) of the total capture and were far more abundant in the Biologically Based treatment (Table 3.1).

Prairie strips harbored different carabid species than the crop field centers (20 m) and supported differential species turnover. Over the full study, 11 species were only found in prairie strips, 6 species were only found in the crop center, and 18 species were found in both habitats (Figure 3.1). Over time, 11 different species which were first found only in prairie strips were also found in the crop center in a subsequent year(s). Only one species first found in the crop center was subsequently found in prairie strips.

Carabid abundance and community structure varied by treatment. The Biologically Based treatment consistently supported higher carabid abundance in all years, due to the prevalence of *Harpalus* species. Overall, the Biologically Based treatment contained 62.5 – 75.2% of the total capture per year, with average captures per trap 1.7 to 3-fold greater than in the Reduced Input treatment (Table 3.2). A non-metric dimensional scaling model (NMDS) by year and treatment graphically show the change in carabid community composition after prairie strips were seeded in 2019 (Figure 3.2; Bray-Curtis dissimilarity, $k = 3$, stress = 0.097). Associated PERMANOVA

analyses show a significant dissimilarity in carabid communities in 2019 ($F_{0,6}$, $p = 0.04$); however, carabid communities in 2020-2022 did not differ significantly (2020: $F_{0,6}$, $p = 0.13$; 2021: $F_{0,6}$, $p = 0.66$; 2022: $F_{0,6}$, $p = 0.08$).

Multiple variables influenced carabid community characteristics. Treatment was a significant factor in carabid activity-density across all years ($p < 0.001$) and within individual years (Table 3.3, 3.4). We tested for seasonal effects, including sampling month on carabid activity-density. Treatments differed only when comparing early/late season (June/September) to mid-season (July/August) (Figure 3.3, 3.4). The model including both treatment and month, but not their interaction, was the best fit; suggesting that carabid phenology is not influenced by treatment.

Seasonal patterns in carabid capture were largely similar from year to year but varied in magnitude. Beetle capture per trap was consistently higher in the Biologically Based treatment than Reduced Input for all years and peaked during July and August, respectively (Figure 3.3). Early and late season activity-density was significantly different than mid-season for both treatments (Figure 3.4). As *Harpalus* species dominate the community in the Biologically Based treatment, abundance was consistently greater than the Reduced Input treatment across months, and highest in July-August when *Harpalus* typically emerges from overwintering (Figure 3.3, 3.4).

Despite turnover in the carabid community, diversity metrics varied little by year 2019-2022. Measured and rarefied species richness estimates were similar within years suggesting that our sampling was sufficient to capture species differences (Table 3.5). The Shannon's Hill diversity (H') for 2019 differed from 2020-2022, indicating effect of year (or crop rotation) since establishment of prairie strips on the carabid community. Diversity metrics for species richness were not significant by treatment ($p < 0.05$); however, Shannon's Hill diversity (H') was significant ($p < 0.001$) (Figure 3.5). The Biologically Based treatment had lower Shannon's Evenness than Reduced Input, likely due to the dominance of *Harpalus* spp. Furthermore, the Biologically Based treatment harbored more singletons and greater species richness than Reduced Input. Species richness and activity-density were positively correlated for both Reduced Input ($F_{0,1} = 79.74$, $p < 0.001$) and Biologically Based ($F_{0,1} = 35.98$, $p < 0.001$). Biologically Based had high activity-density at both low and high species richness, whereas the correlation is more noticeable in Reduced Input (Figure 3.6).

We assessed beta diversity by applying Sorenson's Dissimilarity using treatment and year, which allowed us to further elucidate patterns in the carabid community species turnover and nestedness. Baselga et al. (2010) describes turnover as species replacement resulting from environmental filters or constraints; whereas nestedness refers to species loss, as the community is a subset of more diverse communities. Comparing the carabid communities by center of prairie strip (0 m) vs. field center (20 m), we found the communities in the prairie strips and field centers were highly dissimilar in both treatments (Figure 3.12). Community dissimilarity increased in Reduced Input and nestedness declined, while Biologically Based had decreased dissimilarity and increased nestedness (Figure 3.12).

Spillover Effects

We included distance as a fixed variable in our GLMMs with treatment and month; the best fit model included all variables but not an interaction of distance with month or treatment (Table 3.3). Overall, carabid activity-density in the prairie strips did not differ significantly from 1 m from the strip, however, there were significant differences between 0-5 m ($p < 0.05$) and 0-20 m ($p < 0.05$) across both treatment and year (Table 3.6).

In 2019, the Sorenson's Dissimilarity varied by treatment with Reduced Input less dissimilar (0.4) by sampling location than Biologically Based (0.63) (Table 3.7). By 2022, the dissimilarity by treatment reversed and Reduced Input was notably more dissimilar (0.66) than Biologically Based (0.5). Overall species richness also reflected a similar pattern, as the prairie strip had greater species richness compared to field center in 2019-2020 but reversed by 2021-2022 to greater richness at field center than prairie strip across both treatments (Figure 3.8). Examining the functional traits of the carabid communities revealed additional trends. The only species function that showed a difference among years since prairie strip establishment and management was diet (Figure 3.7). The number of predaceous carabids, though present, stayed consistent from 2019-2022. Omnivores, and particularly granivores, increased after prairie strip establishment and were concentrated in the Biologically Based treatment. Distance was not a significant variable for 2019 for any diet preference. In 2020, the maturing prairie strip resulted in a larger community of omnivores either within (0 m) or near (1 m) the prairie strip compared to further into the row crop (Table 3.9). This is likely due to increased species richness within the transitional zone between the prairie strip and row crops. While omnivorous species maintained higher abundance within or near the prairie strip in 2021-2022, the abundance of predators was

higher at distances within the row crop (Table 3.9). Granivores were more abundant in the Biologically Based treatment, dominated mostly by *H. compar* and *H. pensylvanicus*, with little difference in abundance by distance from the prairie strip. The Biologically Based treatment has historically higher concentrations of giant foxtail (*Setaria faberi* Herrm) than Reduced Input (Figure 3.11), a seed known to be favored by *Harpalus* species and a possible reason for their dominance.

Overwintering status was largely dominated by adult overwintering species, those that emerge in early-spring and mid-summer. There was also little difference in flight ability among carabids, as most are macropterous or capable of flight to some ability. Only two species were brachypterous (lacking flight muscles): *Pterostichus permundus* (Say) and *Cyclotrachelus sodalis* (LeConte) found primarily in the Biologically Based treatment (Table 3.1).

DISCUSSION

Carabid Community Composition

Perennial prairie strips established in two conservation-oriented treatments at the KBS-LTER resulted in increased biodiversity and abundance of carabids, beneficial arthropods that serve as indicator species in agricultural landscapes. Our results demonstrate that prairie strips in row crop agriculture increased overall carabid activity-density and species turnover and both were strongly dependent on cropping treatment. One year after seeding the prairie strips, carabid abundance doubled in both the Reduced Input and Biologically Based treatments. While it is not uncommon for carabids to quickly respond to the introduction of new habitat, as found in Killewald et al. (2023), overall carabid abundance remained high in the third- and fourth-year post-establishment. Several studies (Moschini et al. 2012; Killewald et al. 2023) suggest that the response to natural habitat by beneficial arthropods is independent of management in conventional vs. organic systems. In contrast, many studies corroborate our findings that long-term cropping management results in distinct carabid communities (Clark et al. 1997; Legrand et al. 2011; Boinot et al. 2024; Fiser et al. 2025), and thus management influences community response to the establishment and maturation of perennial prairie strips.

Carabid communities in the Biologically Based treatment have historically supported large populations of granivores, in part due to a build-up of weed seeds (favored by dominant *Harpalus* species) in the seedbank and lack of chemical management (Clark et al. 1997; KBS-LTER agronomy log) (Figure 3.S1). Indeed, organic farming systems have been shown to

increase plant and arthropod species richness compared to conventional practices, particularly for rare species (Gabriel et al. 2006). We found that the Biologically Based treatment initially harbored more singletons in 2019 and a dominant population of *Harpalus* species compared to Reduced Input because of long-term cropping management (Fiser et al. 2025) and less likely the nascent prairie strips established earlier that season. The introduction of prairie strips in the Biologically Based treatment augmented the provision of resources and overall biodiversity.

Prairie Strip Spillover Effects

The establishment of perennial non-crop habitat within high-intensity agricultural landscapes has proven to increase biodiversity of beneficial arthropods (Landis 2000; Tschartnke et al. 2012; Haan et al. 2021). This is likely due to available nesting habitat, protection from predators, and diverse floral or prey resources (Kremen et al. 2020). Large-bodied granivorous species such as *H. compar* and *H. pensylvanicus* dominated the carabid communities in the Biologically Based system and maintained high populations in both the prairie strip and crop field in 2022. We found high numbers of omnivorous carabids, such as those in the genera *Anisodactylus*, *Harpalus*, and *Amara* both in the prairie strips and in the transitional zone 1 m from strip edge. Interestingly, we found a higher abundance of small, predaceous beetles in the genera *Acupalpus*, *Agonoleptus*, and *Elaphropus* throughout the crop field only after prairie strip establishment. It is likely that the prairie strips led to increased populations of omnivorous species, particularly in the “transitional” zone between strip edge and row crop. These beetles would find both food and protection within the prairie strip and, given their small size and limited dispersal ability, could easily travel the short distance between crop and strip for additional resources.

Our models suggest the carabid communities significantly differ between the prairie strip and row crop for both cropping treatments. On the surface, these results could imply limited mixing of the communities. Upon further analysis, we found the model results masked the large species turnover between the prairie strip and field. Although initially found in the prairie strip, 11 species including both omnivorous and predaceous beetles migrated to the field and were only found in field center by 2022. Furthermore, overall species richness shifted from higher in the prairie strip in 2020 to higher in the field by 2022. Thus, our results suggest that prairie strips in row crop agriculture can increase overall biodiversity and result in beneficial spillover effects for both abundance and diversity of carabids in the row crop. Carabids are typically univoltine (one

generation per year), and their presence in the field suggests they may have overwintered at field center. As many of the species found in the row crop in 2022 are predators, these species may also provide necessary pest suppression services for farmers.

Despite greater abundance in the Biologically Based treatment, seasonal differences were consistent across both treatments. In the early and late season (June and September), abundance in the prairie strips was significantly higher than the adjacent row crop; however, mid-season (July-August) had higher abundance throughout the strip and field. This further suggests that prairie strips are serving as valuable refuge habitat for carabids prior to- and after-harvest in row crops. In high-intensity agriculture, the placement of prairie strips may then provide necessary refuge for beneficial arthropods and subsequent natural pest suppression.

A concern for the placement of non-crop habitat within agricultural landscapes, such as perennial prairie strips, is the potential they may act as ecological sinks or traps (Ganser et al. 2019; Schmied et al. 2022). As prairie strips are a relatively new practice in the Midwest, scientists are now studying if and when this may occur. Despite concerns for the contamination of prairie strips from adjacent pesticide use, a study in Iowa found that contour prairie strips had non-lethal levels of neonicotinoids in both soil and plant tissue; further, prairie strips did not reduce the level of neonicotinoids within downhill corn crop (Rutkowski et al. 2024). Schmied et al. (2022) further found that wildflower strips increased pollinator abundance and diversity. However, a study in Missouri detected low levels of neonicotinoids in non-target marginal lands and concluded that reduced wild bee diversity in these areas may be due to nearby pesticide use (Main et al. 2020). Ganser et al. (2019) found that wildflower strips were only an ecological sink for carabids and spiders if ploughed annually. Future research on negative spillover effects are necessary, but many studies have shown that increasing the level of native refuge within high-intensity or simplified agricultural landscapes is necessary for arthropod diversity and ecosystem provision.

Limitations

Our study demonstrates that long-term data is needed to determine the effect of intensive agricultural practices on beneficial arthropods and the implications for conservation interventions such as prairie strips. Future research should address potential limitations of this study design. First, prairie strips were placed in only two conservation-oriented treatments at the LTER, excluding the high-input and no-till conventional treatments. Second, carabid communities prior

to 2019 and the establishment of the prairie strips were not sampled; however, due to the limited effect of the nascent prairie strip in the first year and previous work on the communities in 2019 (see Fiser et al. 2025), we do not believe the 2019 carabid community varied from the year prior to strip establishment.

Insufficient sampling is also unlikely given that our coverage estimates for species diversity were > 95% of sampled biodiversity across all years of sampling. Year since prairie strip establishment also coincides with crop rotation, and we understand that insect communities may fluctuate in short time intervals. Further long-term sampling at the LTER will elucidate potential patterns in insect communities.

CONCLUSION

Prairie strips are a valuable conservation tool to enhance biodiversity of beneficial arthropods in agricultural landscapes. Our study demonstrates that mature prairie strips harbor unique species and contribute to the spillover of biodiversity to adjacent row crops. As carabids are indicators for ground-dwelling arthropods, farmers investing in conservation interventions may benefit from increased pest and weed suppression.

Prairie strips offer one solution to meet these goals, by introducing natural refuge into otherwise highly simplified landscapes to increase wildlife biodiversity and dispersal while benefiting farming communities through ecosystem service provision. Many nations now have federal policies that incentivize farmers and land-owners to adopt conservation practices in agriculture to mitigate the effects of ongoing climate change and create resilient agricultural systems for the future. Continued research on the services or potential disservices of prairie strips within high-intensity agricultural landscapes is necessary to meet these goals.

Research on the impacts of arthropod communities within agricultural landscapes is not possible without long-term scientific funding to support stations such as the KBS-LTER and the many researchers dedicated to improving the health and sustainability of agricultural systems for food security, human well-being, and ecosystem health.

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APPENDIX A. CHAPTER THREE FIGURES AND TABLES

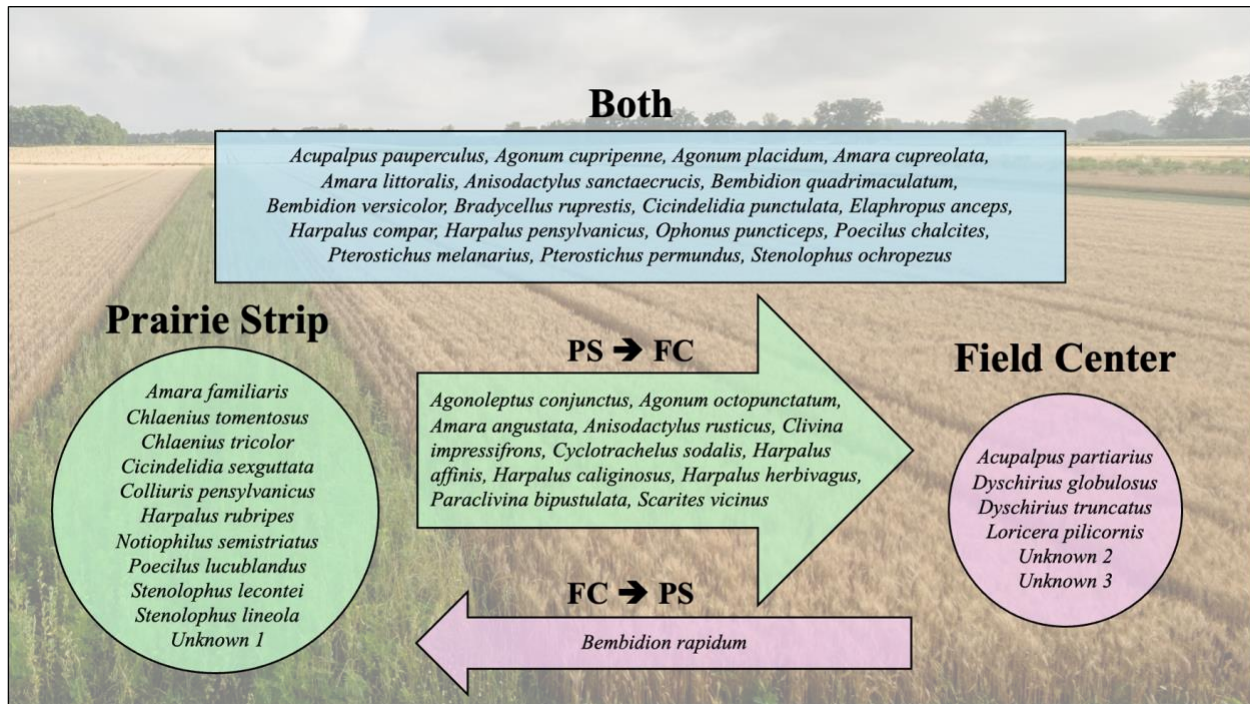


Figure 3.1. Graphic demonstrating species unique to the prairie strip (PS), field center (FC) = 20 m from strip edge, and both locations from 2019-2022 within the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. In total, 11 species occurred only in the prairie strip, 6 species in the field center, and 18 species within both; 11 species were initially found in the strip in 2019 and only found at field center by 2022, while only one species was initially found at field center and moved to the strip by 2022. Results indicate prairie strips increase biodiversity within cropping systems. Photo Credit: Kurt Stepnitz

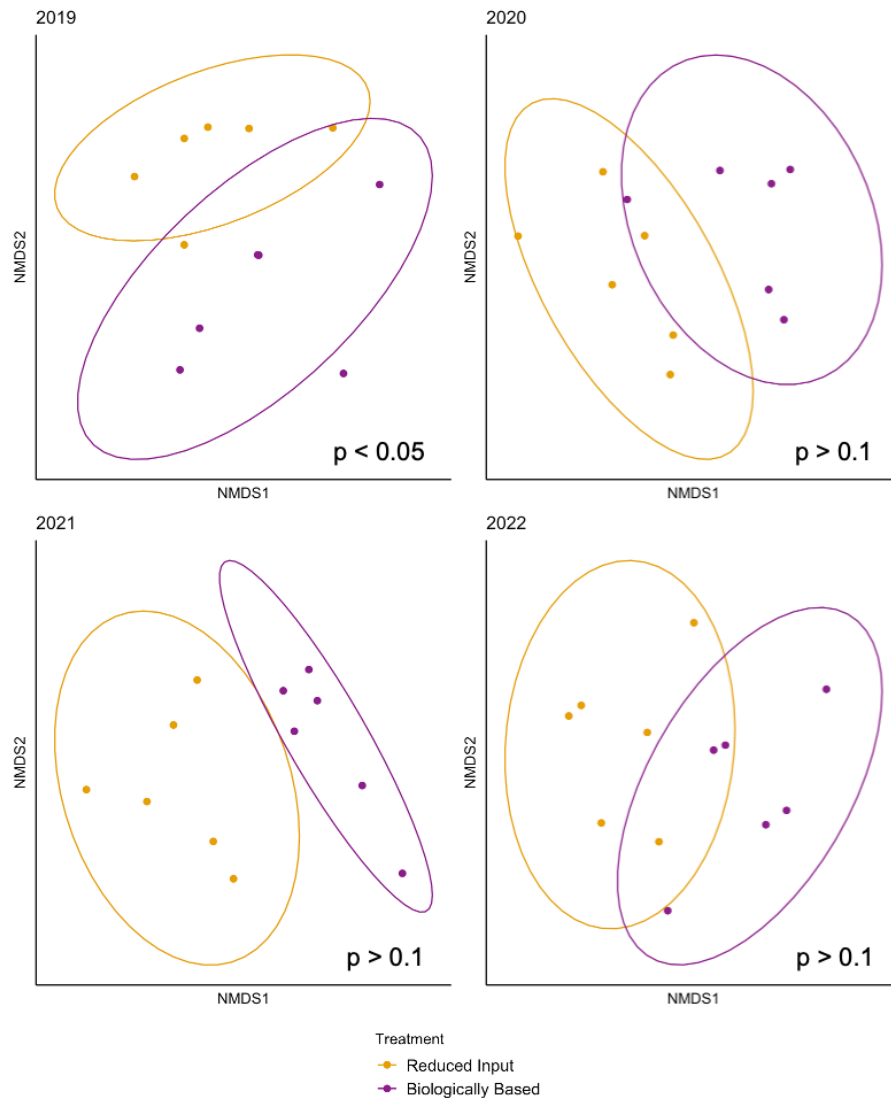


Figure 3.2. Non-metric Multidimensional Scaling (NMDS) graphical comparison of 2019-2022 carabid community composition by treatment. The NMDS plot (Bray-Curtis dissimilarity, $k = 3$, stress = 0.097) illustrates that community composition differs between Reduced Input (light blue) and Biologically Based (light green) treatments within the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. PERMANOVA results show significant differences among treatment types for 2019 vs. 2022 ($F_{0,1}$, $p = 0.033$).

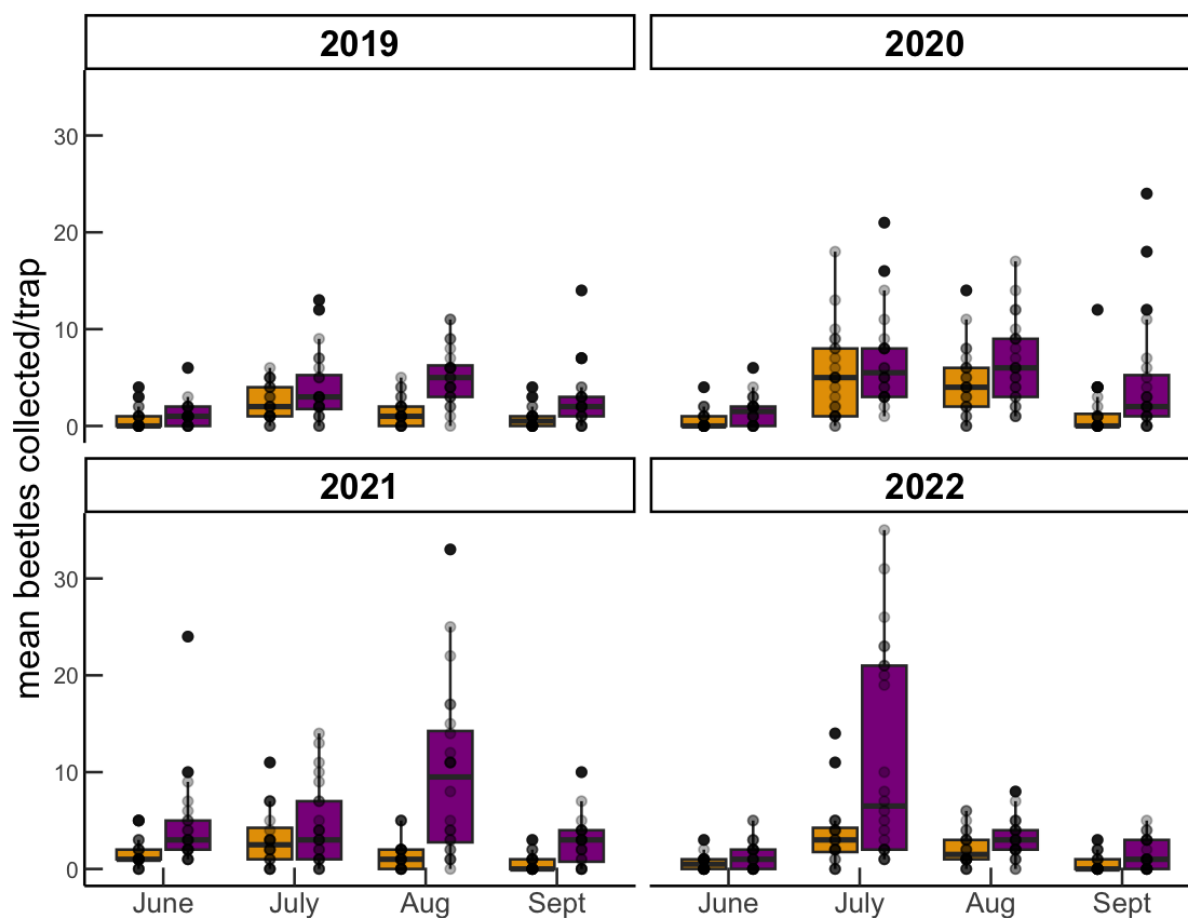
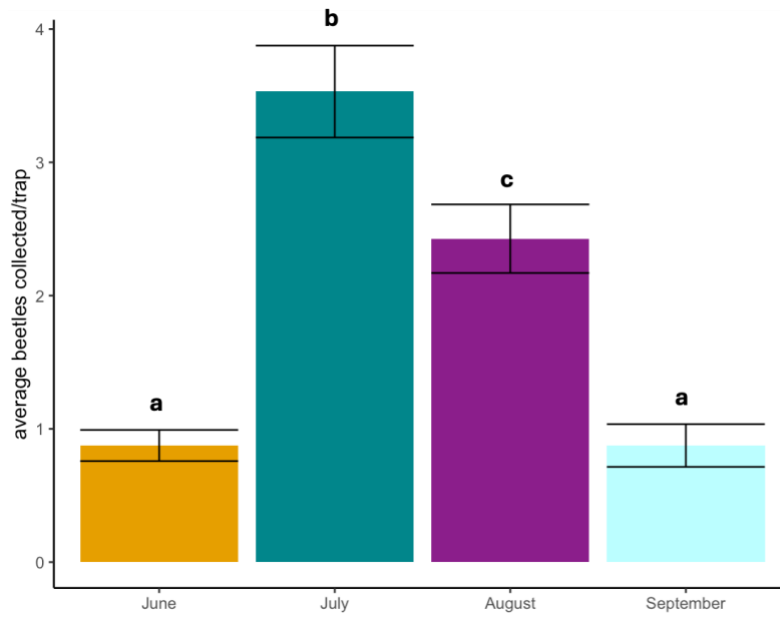


Figure 3.3. Comparison of carabid activity-density (abundance) for 2019 - 2022 by month and treatment. Beetles collected per trap were consistently higher in the Biologically Based treatment than Reduced Input for all years and peaked during July and August, respectively. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

A) Reduced Input



B) Biologically Based

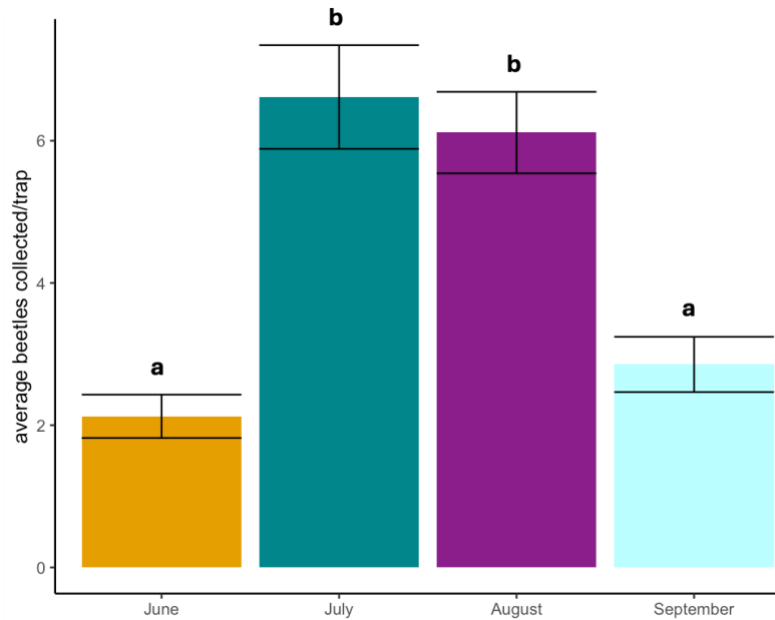


Figure 3.4. Average beetles collected per trap for 2019 - 2022 by month for A) Reduced Input and B) Biologically Based. Using ANOVA tests, early and late season activity-density was significantly different than mid-season for both treatments. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

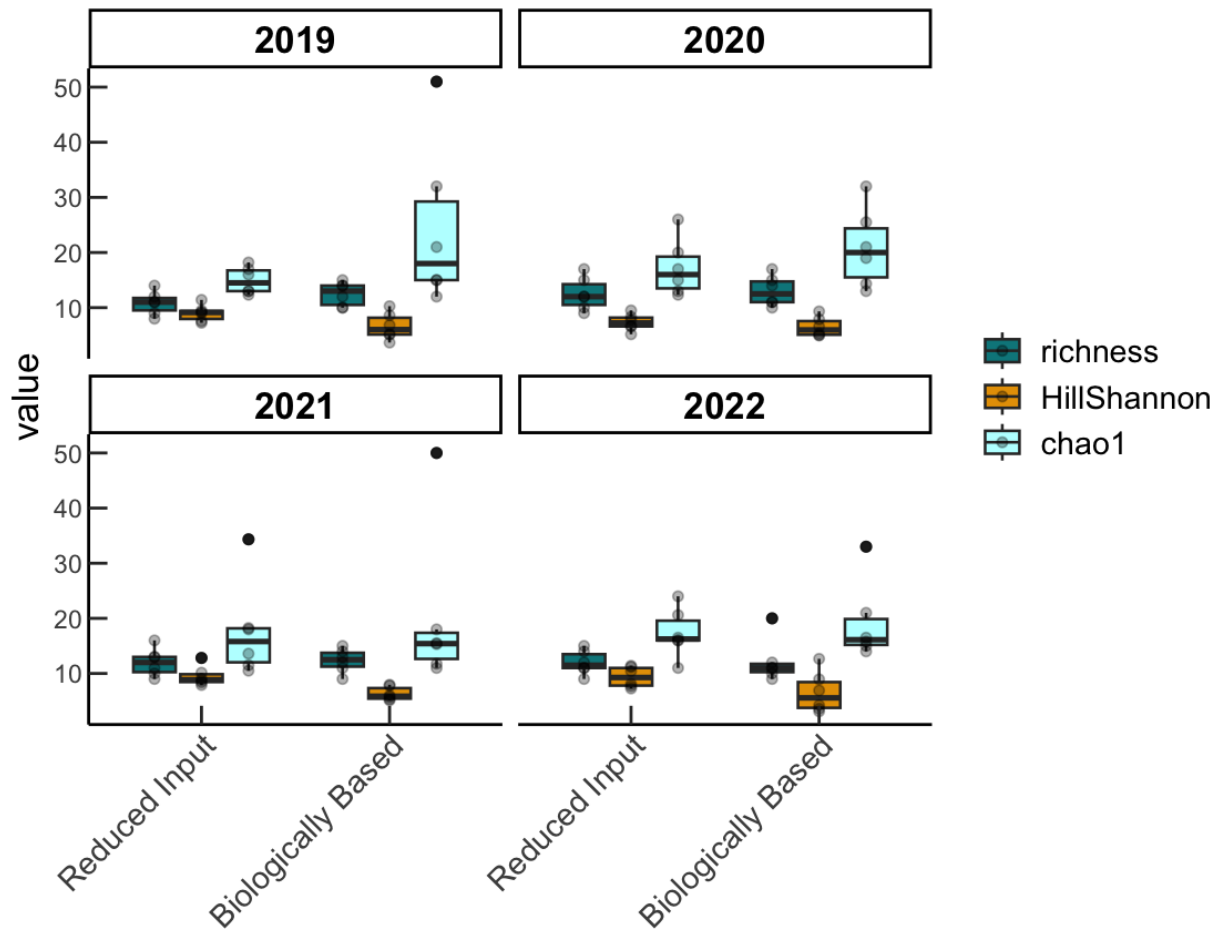


Figure 3.5. Diversity metrics by treatment (Reduced Input and Biologically Based) for 2019-2022, including species richness, Shannon’s Hill Diversity, and Chao1 estimate of richness. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

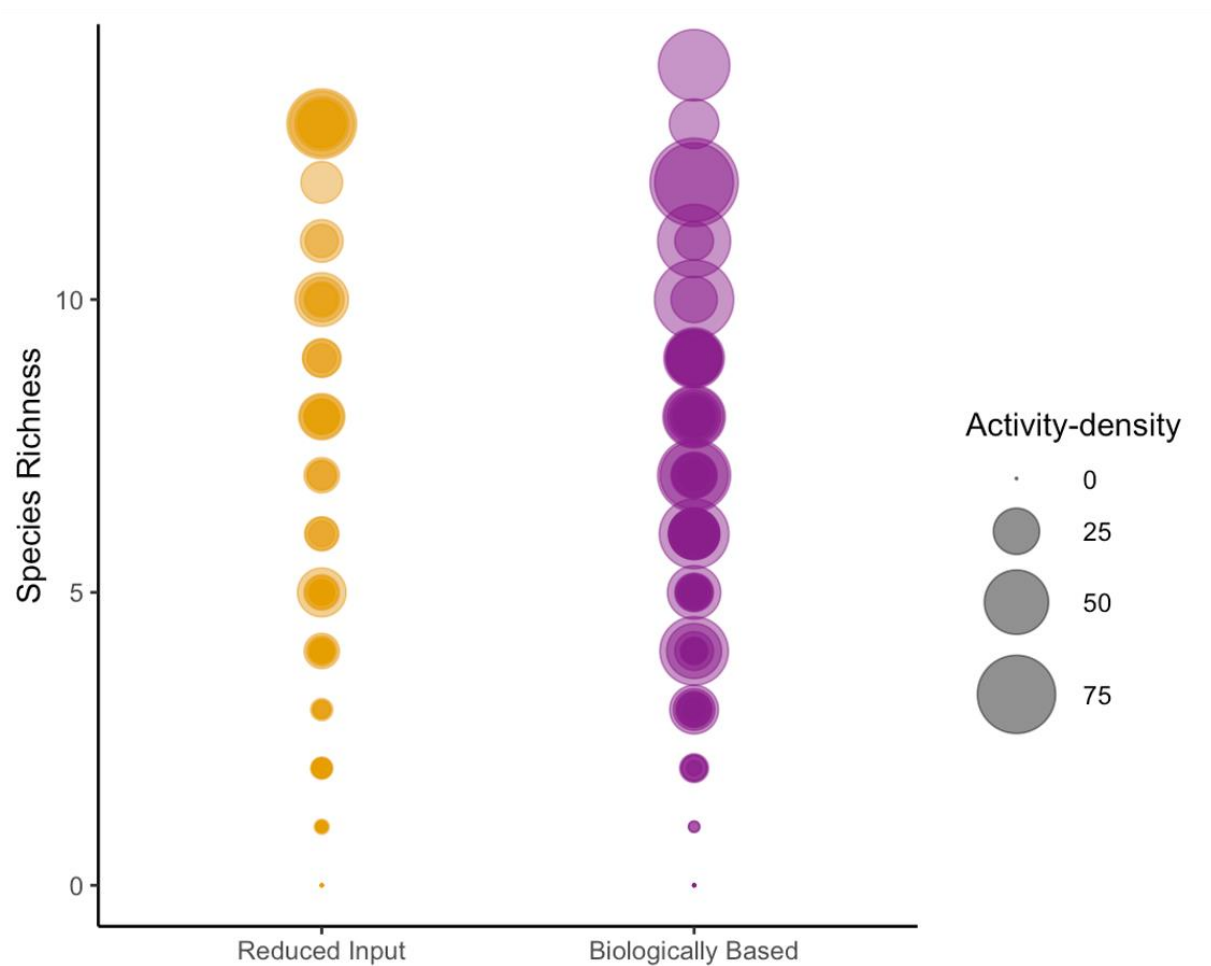


Figure 3.6. Visual representation of species richness and activity-density (abundance) by cropping treatment. Using analysis of variance (AOV), species richness (y axis) and activity-density (circle diameter) are significant for both Reduced Input and Biologically Based. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

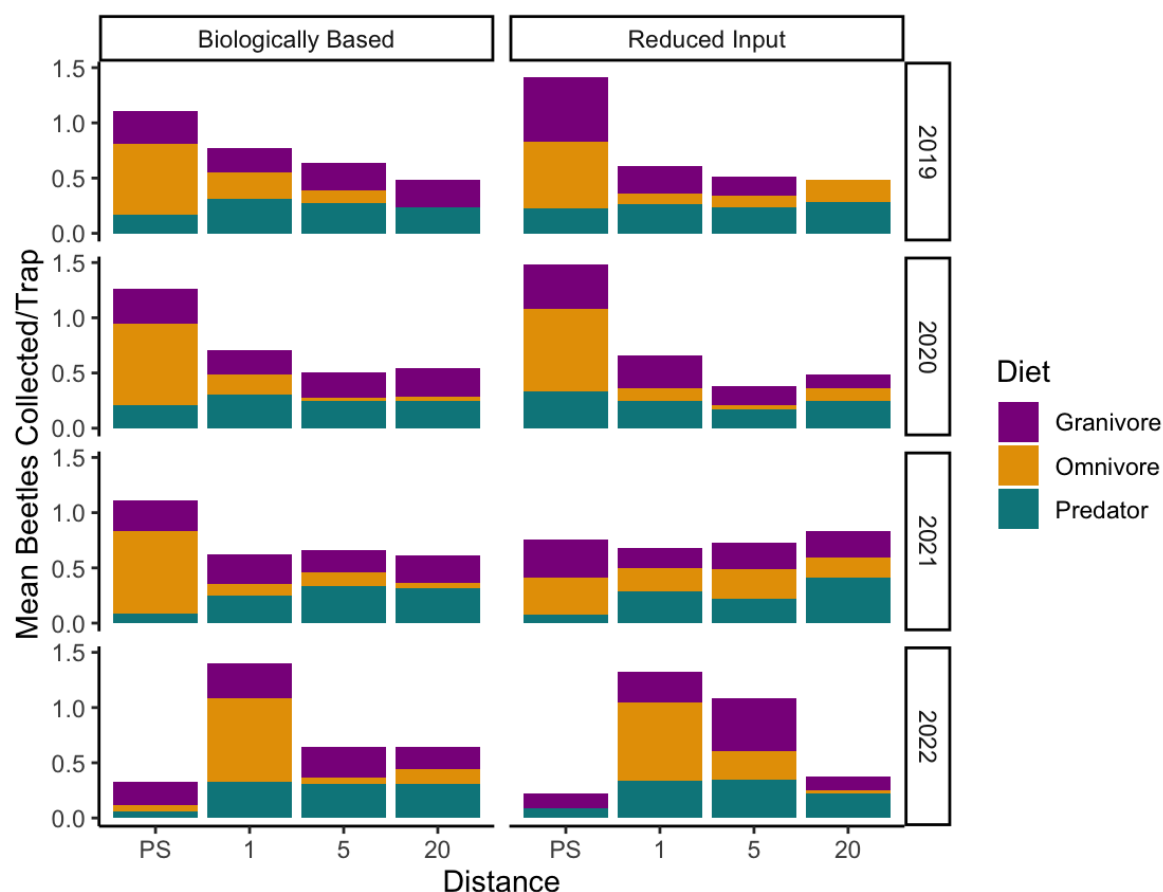


Figure 3.7. Description of carabid diet by year (2019-2022), treatment (Reduced Input vs. Biologically Based) and distance (0m or within strip and 1,5, and 20 m from strip edge) and the average beetle collected per trap. Diet delineation is defined as their primary diet choice (i.e. P/O is listed as Predator not both). Granivorous carabids were collected at higher rates in the Biologically Based treatment either within or near the prairie strip (PS or 1 m) as compared to Reduced Input in years after strip establishment. Kellogg Biological Station Long-term Ecological Research main-station in Hickory Corners, MI.

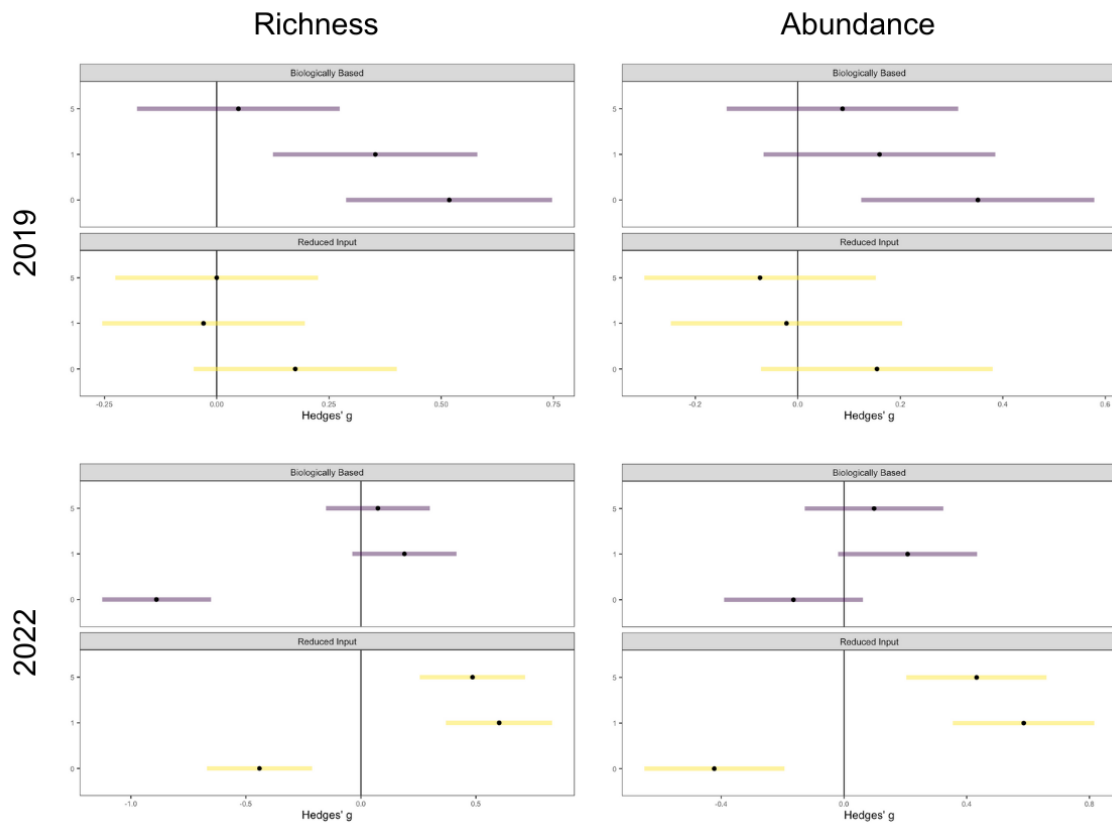


Figure 3.8. Hedge's g effect size demonstrating difference in carabid species richness (left) and abundance (activity-density) (right) at distances 0 m (within prairie strip), 1, and 5 m from strip edge to a baseline for abundance at field center (20 m from strip edge) across both treatments in 2019 and 2022 at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI (Robertson and Hamilton, 2015).



Figure 3.9. Experimental design for the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI (Robertson and Hamilton 2015).

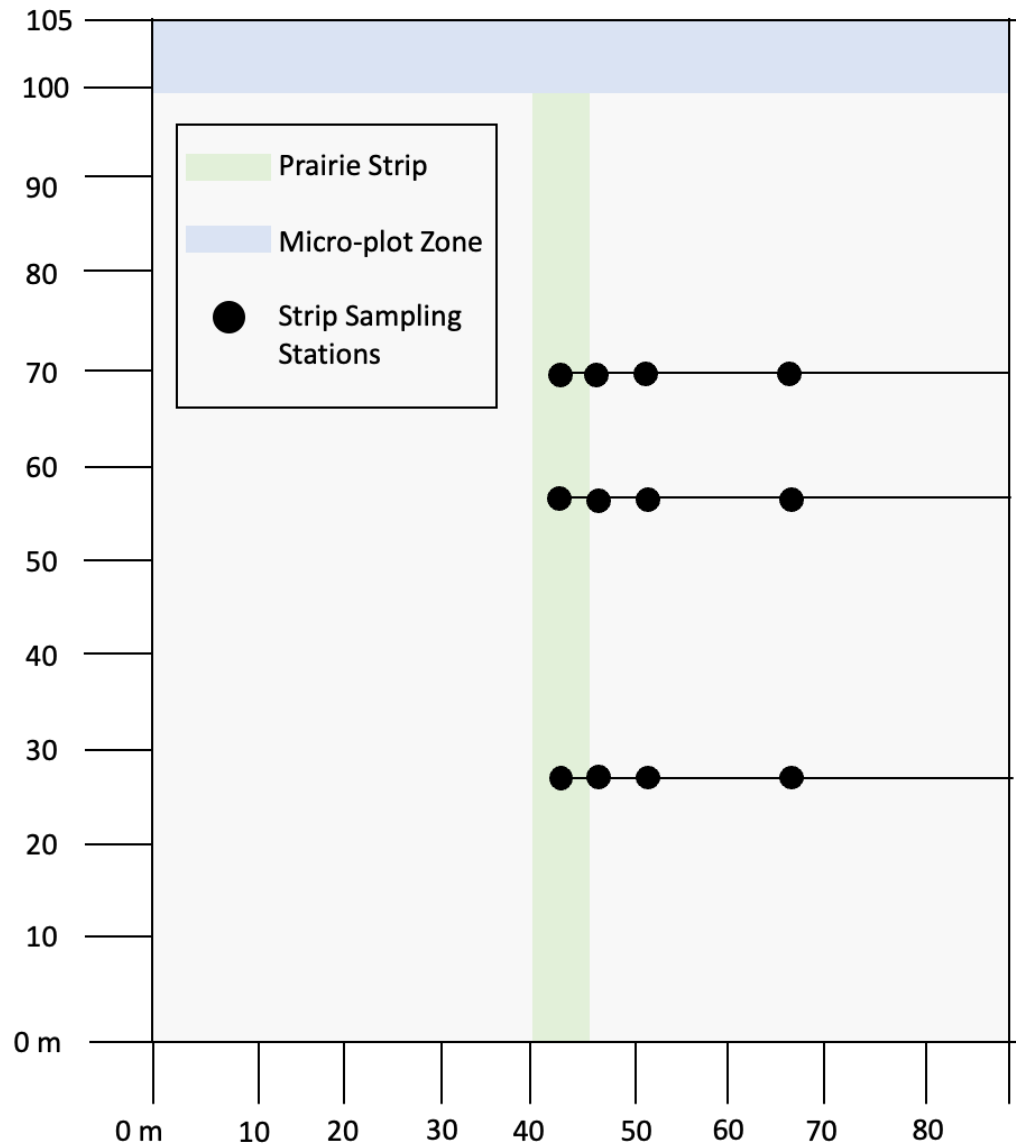


Figure 3.10. Experimental design for 2019 pitfall trap sampling showing three transects (North, Central, South) and sampling stations placed at varying distances from prairie strip (0, 1, 5, and 20 m), and the five 1994-95 sampling stations for the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

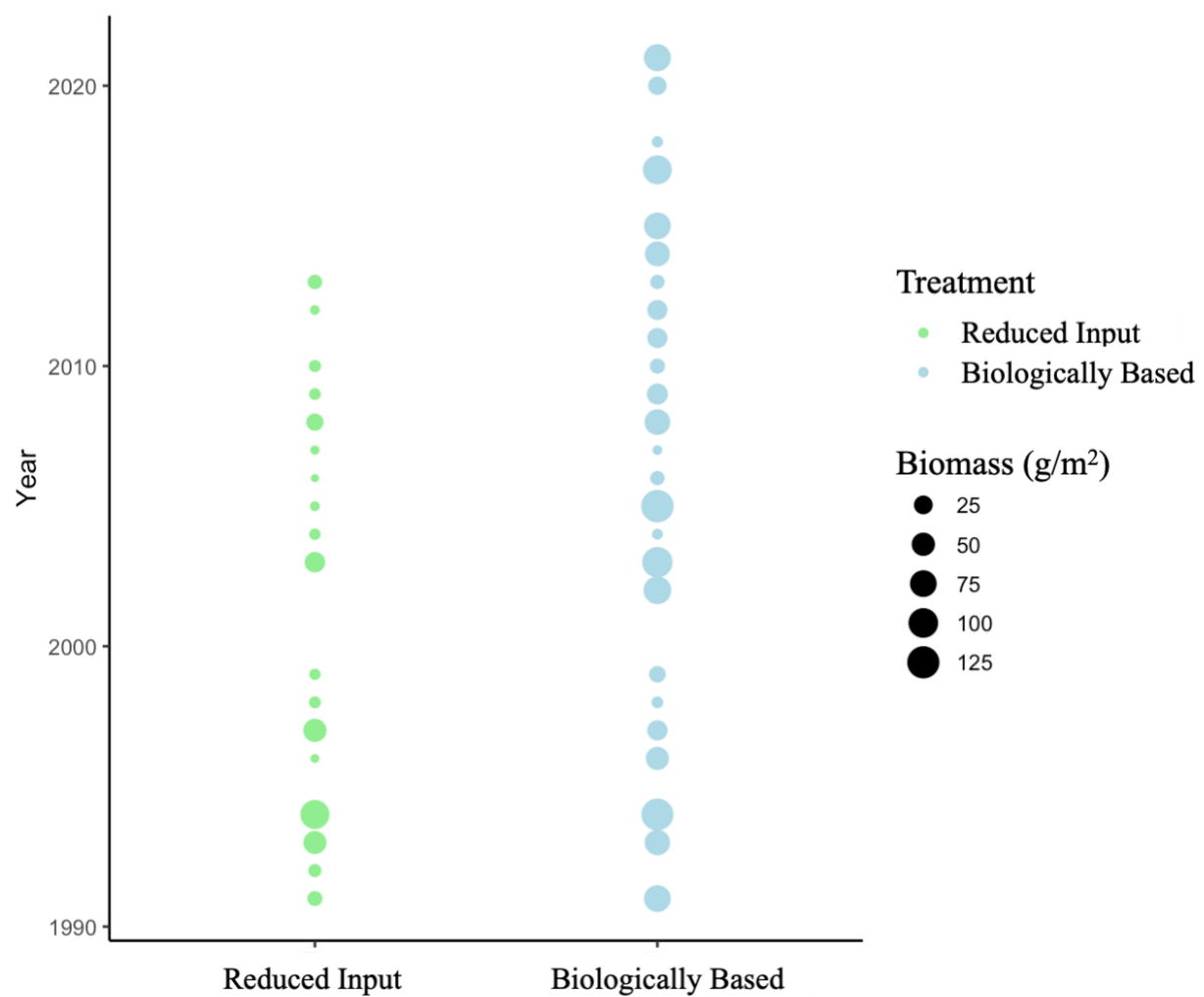


Figure 3.11. Visual representation of the common weed Foxtail (*Setaria faberi* herzm.) density (g/m²) from 1990 – 2022 for Reduced Input and Biologically Based treatments. Foxtail was eliminated from Reduced Input by 2019 but persists in the Biologically Based treatment through 2022. Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. Weed data courtesy of KBS-LTER data manager Sven Bohm.

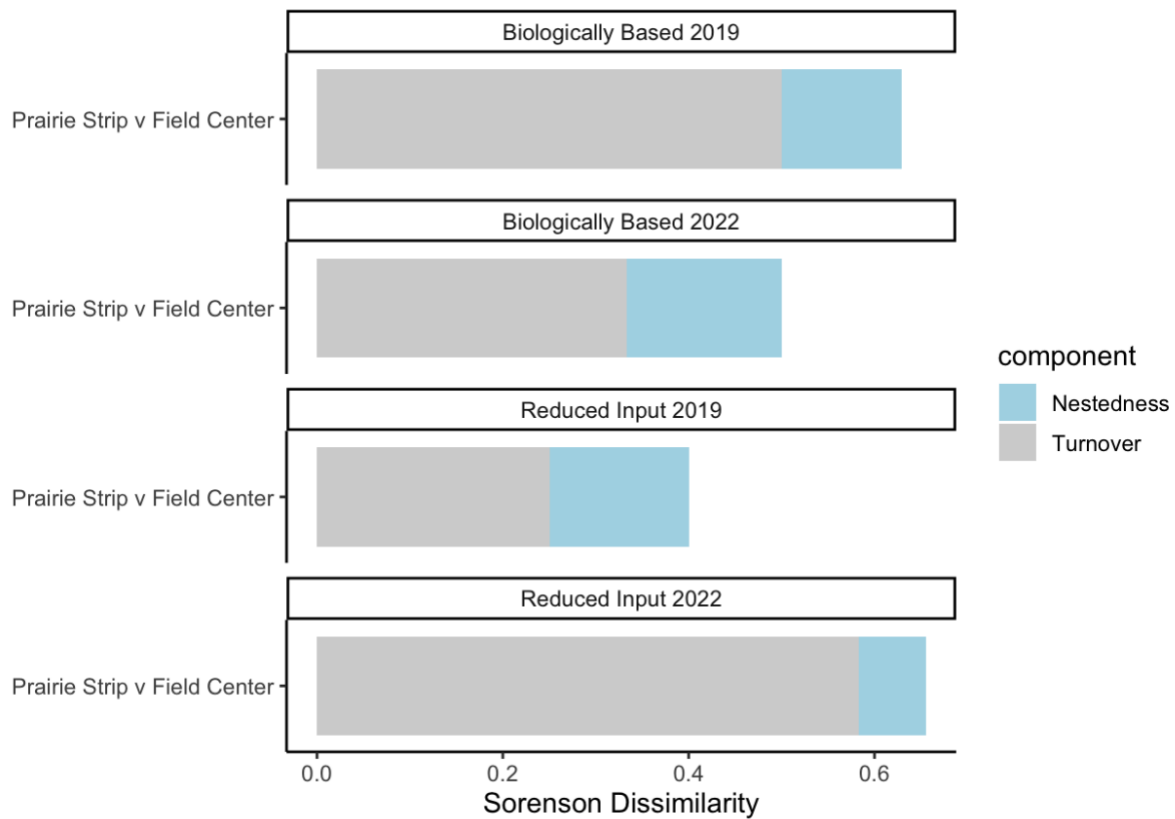


Figure 3.12. Nestedness and species turnover of the carabid community at the KBS-LTER 2019 vs 2022 by treatment. Community dissimilarity increased in Reduced Input while Nestedness declined, whereas the Biologically Based treatment had decreased dissimilarity and increased Nestedness.

Table 3.1. Summary table of carabid species captured including functions (diet, overwintering status, and flight ability) by year and species. Diet is described as Predator (P), Omnivore (O), or Granivore (G) or unknown; overwintering is described as Adult (A), Larval (L), or Unknown (UK); flight is described as Brachypterous (B, incapable of flight) or Macropterous (M, capable of flight), or Unknown (UK). Samples collected from 2019-2022 at the Kellogg Biological Station Long-term Ecological Research Main Copping Systems Experiment, Hickory Corners, MI.

Species Name	Function			2019		2020		2021		2022	
	Diet	OW	Flight	RI	BB	RI	BB	RI	BB	RI	BB
<i>Acupalpus partiaris</i>	P	UK	UK	0	0	0	0	0	0	2	6
<i>Acupalpus pauperculus</i>	P	A	M	0	0	1	12	4	13	3	1
<i>Agonoleptus conjunctus</i>	P	A	M	2	3	0	0	0	1	0	0
<i>Agonum cupripenne</i>	P	A	M	1	1	0	3	0	0	2	0
<i>Agonum octopunctatum</i>	P	A	M	0	1	0	1	0	0	1	0
<i>Agonum placidum</i>	P/O	A	M	9	5	0	0	2	0	0	2
<i>Amara angustata</i>	G/O	A	M	0	0	2	2	0	0	4	0
<i>Amara cupreolata</i>	G/O	A	M	0	0	4	2	6	10	2	4
<i>Amara familiaris</i>	O	A	M	2	13	0	0	0	0	0	0
<i>Amara littoralis</i>	O	A	M	4	10	2	3	0	0	0	1
<i>Amara pensylvanicus</i>	O	A	M	0	1	0	0	0	0	0	0
<i>Anisodactylus rusticus</i>	O	A	M	0	5	15	69	8	61	19	13
<i>Anisodactylus sanctaecrucis</i>	O	A	M	3	0	62	15	22	4	7	2
<i>Bembidion quadrimaculatum</i>	P	A	M	4	5	17	3	22	22	11	4
<i>Bembidion rapidum</i>	P	A	M	0	2	2	2	6	0	1	0
<i>Bembidion versicolor</i>	P	A	M	10	5	0	0	5	9	3	1
<i>Bradycellus rufestis</i>	P	A	M	2	0	11	2	3	4	4	5
<i>Chlaenius tomentosus</i>	O	A	M	0	0	1	0	0	0	3	1
<i>Chlaenius tricolor</i>	P	A	M	6	0	2	1	0	0	5	2
<i>Cicindelidia punctulata</i>	P	L	M	16	23	3	9	13	3	35	24
<i>Cicindelidia sexguttata</i>	P	UK	UK	0	0	0	0	0	0	0	1
<i>Clivina impressifrons</i>	P/O	A	M	0	1	0	1	0	3	1	1
<i>Colliuris pensylvanicus</i>	P	A	M	0	1	0	0	0	0	0	0
<i>Cratacanthus dubius</i>	P	A	M	0	0	0	0	1	1	0	2
<i>Cyclotrachelus sodalis</i>	P/O	L	B	2	2	1	1	4	3	7	7
<i>Dyschirius globulosus</i>	P	UK	UK	0	0	0	0	0	0	1	0
<i>Dyschirius truncatus</i>	P	A	M	0	1	0	0	0	0	0	0
<i>Elaphropus anceps</i>	P/O	A	M	4	5	1	9	10	8	11	7
<i>Harpalus affinis</i>	G/O	A	M	1	1	5	1	3	1	6	1
<i>Harpalus caliginosus</i>	G/O	A	M	0	2	0	4	0	0	0	1
<i>Harpalus compar</i>	G/O	A	M	4	117	10	121	3	168	8	187
<i>Harpalus herbivagus</i>	G/O	A	M	0	1	0	7	0	7	0	0
<i>Harpalus pensylvanicus</i>	G/O	L	M	8	73	77	135	9	128	1	104
<i>Harpalus rubripes</i>	O	A	M	0	2	0	0	0	0	0	0
<i>Loricera pilicornis</i>	P	A	M	2	3	0	0	0	0	0	0
<i>Notiophilus semistriatus</i>	P	A	M	0	0	0	0	0	1	0	0
<i>Ophonus puncticeps</i>	G	L	M	0	0	0	0	1	0	2	1
<i>Paraclivina bipustulatus</i>	P	A	M	0	0	5	5	4	2	0	2
<i>Poecilus chalcites</i>	P/O	A	M	22	22	35	45	29	50	11	23
<i>Poecilus lucublandus</i>	P/O	A	M	3	0	2	1	0	0	0	0
<i>Pterostichus melanarius</i>	P	L	M	12	1	9	5	8	0	7	2
<i>Pterostichus permundus</i>	P/O	A	B	0	1	9	3	4	2	0	2
<i>Scarites vicinus</i>	P	A	M	0	3	1	1	1	5	0	6
<i>Stenolophus lecontei</i>	P/O	A	M	0	0	1	0	0	0	0	0
<i>Stenolophus lineola</i>	P/O	A	M	0	0	1	0	1	0	0	0
<i>Stenolophus ochropepus</i>	P/O	A	M	12	2	6	1	0	3	9	0
<i>Stenolophus plebejus</i>	P	A	M	2	0	0	0	0	0	0	0
<i>Unknown 1</i>	UK	UK	UK	0	0	0	0	0	0	1	0
<i>Unknown 2</i>	UK	UK	UK	0	0	0	0	0	0	0	1
<i>Unknown 3</i>	UK	UK	UK	0	0	0	0	0	0	0	1
Total				131	312	285	464	169	509	167	415

Table 3.2. Summary of sample mean and standard error of the mean for 2019-2022 (excluding May samples) by treatment (Reduced Input and Biologically Based). Mean beetle catch per trap increased after prairie strip establishment (2020-2022), particularly in the Biologically Based treatment. Kellogg Biological Station Long-term Ecological Research Main Cropping Systems Experiment in Hickory Corners, MI.

Year	Treatment	Total	Sample Mean +/- se
2019 <i>wheat</i>	Reduced Input	131	0.45 ± 0.25
	Biologically Based	311	1.08 ± 0.59
	ALL	442	0.77 ± 0.32
2020 <i>corn</i>	Reduced Input	279	0.97 ± 0.58
	Biologically Based	465	1.61 ± 0.87
	ALL	744	1.29 ± 0.52
2021 <i>soybean</i>	Reduced Input	167	0.58 ± 0.32
	Biologically Based	506	1.76 ± 0.97
	ALL	673	1.17 ± 0.51
2022 <i>wheat</i>	Reduced Input	163	0.57 ± 0.34
	Biologically Based	418	1.45 ± 0.99
	ALL	581	1.01 ± 0.53

Table 3.3. Generalized Linear Mixed Methods (GLMM) negative binomial models were developed for 2019-2022 carabid abundance (activity-density) based on known variables for treatment (Reduced Input vs. Biologically Based), month (June-September), and distance (0 m or within strip and 1,5, and 20 m from strip edge), as well as the interactions between distance and treatment (D:T) or month and treatment (M:T). The models were ranked via their QAICc values and overall weight. The negative binomial model takes into consideration zero-inflation.

Best Model: abundance ~ treatment + month + distance + (1 rep)							
Variable							
Treatment	Month	Distance	D:T	M:T	df	QAICc	Weight
+	+	+			11	3460.6	0.646
+	+	+		+	15	3462.0	0.320
+	+	+	+		14	3466.5	0.035
	+				7	3577.1	0.0
+					4	3905.1	0.0
		+			6	3972.3	0.0
					3	3972.5	0.0

Table 3.4. Summary of 2019-2022 Generalized Linear Mixed Methods (GLMM) negative binomial models for carabid abundance (activity-density) and ANOVA test for treatment as the key variable (Reduced Input vs. Biologically Based).

Year	SE	z.ratio	p-value
2019 <i>wheat</i>	0.05	16.93	< 0.001
2020 <i>corn</i>	0.05	16.93	< 0.001
2021 <i>soybean</i>	0.04	23.93	< 0.001
2022 <i>wheat</i>	0.15	-5.69	< 0.001

Table 3.5. Summary of diversity metrics for 2019-2022 (excluding May samples) including Shannon's Diversity (H), Evenness (E), and Rarefaction (R) by treatment (Reduced Input and Biologically Based). Kellogg Biological Station Long-term Ecological Research Main Cropping Systems Experiment in Hickory Corners, MI.

Year	Treatment	Genus	Species	R	H	E
2019 <i>wheat</i>	Reduced Input	15	23		2.74	0.89
	Biologically Based	17	29		2.13	0.63
	ALL	19	34	34	2.54	0.72
2020 <i>corn</i>	Reduced Input	15	25		1.27	0.39
	Biologically Based	17	29		1.61	0.48
	ALL	17	29	28.7	2.37	0.69
2021 <i>soybean</i>	Reduced Input	17	23		1.02	0.33
	Biologically Based	18	23		1.74	0.56
	ALL	20	28	26.2	2.42	0.73
2022 <i>wheat</i>	Reduced Input	17	26		1.13	0.35
	Biologically Based	18	29		1.56	0.46
	ALL	20	37	34.6	2.37	0.66

Table 3.6. Summary of post-hoc pairwise tests performed using the “emmeans” function in the R package *emmeans* (Lenth et al., 2023) to determine significant pairwise differences within the best fit model for distance from prairie strip (0 m or within strip, and 1, 5, and 20 m from strip edge) across both treatments 2019-2022. Kellogg Biological Station LTER Main Cropping Systems Experiment, Hickory Corners, MI.

(m)	0	1	5
1	0.66	-	-
5	0.014	0.235	-
20	0.037	0.41	0.987

Table 3.7. Number of species by sample location, either in the prairie strip (PS), field center (FC), or both from 2019-2022 in both treatments (Reduced Input and Biologically Based), and calculated Sorenson’s Dissimilarity. All samples collected at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

A) 2019 (wheat)

Treatment	(Both)	PS	FC	SD
Reduced Input	9	9	3	0.4
Biologically Based	5	12	5	0.63
All	12	13	5	0.43

B) 2020 (corn)

Treatment	(Both)	PS	FC	SD
Reduced Input	8	10	5	0.48
Biologically Based	10	10	3	0.4
All	15	12	2	0.32

C) 2021 (soybean)

Treatment	(Both)	PS	FC	SD
Reduced Input	7	3	9	0.46
Biologically Based	10	4	6	0.33
All	13	3	9	0.32

D) 2022 (wheat)

Treatment	(Both)	PS	FC	SD
Reduced Input	5	7	12	0.66
Biologically Based	8	4	12	0.5
All	12	5	16	0.47

Table 3.8. Species richness for the Reduced Input and Biologically Based treatments by distance from prairie strip (PS) or field center (FC) from 2019-2022. All samples collected at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI.

A) 2019 (wheat)

Treatment	All	PS	FC
RI	21	18	12
BB	22	17	10
All	30	25	18

B) 2020 (corn)

Treatment	All	PS	FC
RI	23	18	13
BB	23	20	13
All	29	27	17

C) 2021 (soybean)

Treatment	All	PS	FC
RI	19	10	16
BB	20	14	16
All	25	16	22

D) 2022 (wheat)

Treatment	All	PS	FC
RI	24	12	17
BB	24	12	20
All	33	17	28

Table 3.9. Summary of mean (\pm SE) beetles collected per trap by diet (Predator, Granivore, Omnivore) by distance from prairie strip (0m within strip, 1, 5, and 20 m from strip edge) for 2019-2022. Kellogg Biological Station LTER Main Cropping Systems Experiment, Hickory Corners, MI.

Diet	Distance from Prairie Strip (m)			
	0	1	5	20
Predator	0.16 \pm 0.03	0.29 \pm 0.012	0.27 \pm 0.022	0.29 \pm 0.02
Granivore	0.32 \pm 0.047	0.25 \pm 0.02	0.25 \pm 0.03	0.18 \pm 0.03
Omnivore	0.48 \pm 0.11	0.3 \pm 0.1	0.13 \pm 0.03	0.09 \pm 0.03

Table 3.10. Details for agrochemical (fertilizer and pesticide) applications in 2018-2022 in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. See herbicide (<https://lter.kbs.msu.edu/datatables/160>), fertilizer (<https://lter.kbs.msu.edu/datatables/159>), and insecticide applications (<https://lter.kbs.msu.edu/datatables/161>) on the lter.kbs.msu.edu website.

Year	Treatment	Herbicide	Insecticide	Fertilizer
2018	Reduced Input	Herbicide Roundup Power Max (glyphosate 48.7%)	None	Fertilizer 0-0-60 potash fertilizer Ammonium sulfate (AMS)
2018	Biologically Based	None	None	
2019	Reduced Input	Herbicide PowerFlex HL Herbicide Roundup Power Max (glyphosate 48.7%)	NIS (Activator 90)	Fertilizer 28% UAN (28-0-0) Sulfur (0-0-0-85) Fertilizer 0-46-0 phosphate fertilizer Fertilizer 0-0-60 potash fertilizer Ammonium sulfate (AMS) Prairie Strip Custom Seed mix Fertilizer 28% UAN (28-0-0)
2019	Biologically Based	None	None	Prairie Strip Custom Seed mix
2020	Reduced Input	Dual II Magnum (s-metolachlor (+ safener)) Herbicide Roundup Power Max (glyphosate 48.7%)		Fertilizer 0-0-60 potash fertilizer Fertilizer 16.5-16.5-0-2.9 Ammonium sulfate (AMS)
2020	Biologically Based	None	None	None
2021	Reduced Input	Herbicide Roundup Power Max (glyphosate 48.7%)		Fertilizer 0-0-60 potash fertilizer Fertilizer 0-46-0 phosphate fertilizer Ammonium sulfate (AMS)
2021	Biologically Based	None	None	None
2022	Reduced Input	Herbicide PowerFlex HL		Fertilizer UAN 28% Fertilizer 0-46-0 phosphate fertilizer Fertilizer 0-0-60 potash fertilizer Sulfur (0-0-0-85)
2022	Biologically Based	None	None	None

Table 3.11. Prairie Strips perennial mixture, including 18 forbs and 4 warm-season grasses planted in April 2019. Kellogg Biological Station LTER Main Cropping Systems Experiment, Hickory Corners, MI.

Grass Species	Common Name	Seeds/ft²
<i>Andropogon gerardii</i>	Big Bluestem	0.92
<i>Bouteloua curtipendula</i>	Side-oats Grama	1.93
<i>Elymus canadensis</i>	Canada Wild Rye	0.48
<i>Schizachyrium scoparium</i>	Little Bluestem	3.44
	Total	6.77
Forb Species	Common Name	Seeds/ft²
<i>Achillea millefolium</i>	Yarrow	2.05
<i>Asclepias syriaca</i>	Common Milkweed	0.33
<i>Asclepias tuberosa</i>	Butterfly Milkweed	0.30
<i>Aster novae-angliae</i>	New England Aster	1.1.4
<i>Coreopsis lanceolata</i>	Lance-leaf Coreopsis	1.84
<i>Coreopsis tripteris</i>	Tall Coreopsis	0.26
<i>Desmodium canadense</i>	Showy Tick Trefoil	0.25
<i>Echinacea purpurea</i>	Purple Coneflower	0.61
<i>Lespedeza capitata</i>	Round-headed Bush Clover	0.30
<i>Monarda fistulosa</i>	Wild Bergamot	1.21
<i>Ratibida pinnata</i>	Yellow Coneflower	0.69
<i>Rudbeckia hirta</i>	Black-eyed Susan	5.28
<i>Silphium perfoliatum</i>	Cup Plant	0.04
<i>Solidago juncea</i>	Early Goldenrod	2.66
<i>Solidago nemoralis</i>	Old-field Goldenrod	2.75
<i>Tradescantia ohiensis</i>	Common Spiderwort	0.18
<i>Verbena stricta</i>	Hoary Vervain	0.96
<i>Zizia aurea</i>	Golden Alexander	0.72
	Total	21.57

APPENDIX B. RECORD OF DEPOSITION OF VOUCHER SPECIMENS

The specimens listed below have been deposited in the named museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number have been attached or included in fluid preserved specimens.

Voucher Number: _____2025-03_____

Author and Title of thesis:

Cynthia M. Fiser

Effect of conservation-oriented management on carabid (Coleoptera: Carabidae) communities in agricultural landscapes

Museum(s) where deposited:

Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Table 3.12. List of voucher specimens

Family	Genus-Species	Life Stage	Quantity	Preservation
Carabidae	<i>Acupalpus partiaris</i>	adult	3	pinned
Carabidae	<i>Acupalpus pauperculus</i>	adult	3	pinned
Carabidae	<i>Agonoleptus conjunctus</i>	adult	3	pinned
Carabidae	<i>Agonum cupripenne</i>	adult	3	pinned
Carabidae	<i>Agonum octopunctatum</i>	adult	3	pinned
Carabidae	<i>Agonum placidum</i>	adult	3	pinned
Carabidae	<i>Agonum unknown</i>	adult	1	pinned
Carabidae	<i>Amara angustata</i>	adult	3	pinned
Carabidae	<i>Amara cupreolata</i>	adult	3	pinned
Carabidae	<i>Amara familiaris</i>	adult	3	pinned

Table 3.12. (cont'd)

Family	Genus-Species	Life Stage	Quantity	Preservation
Carabidae	<i>Amara littoralis</i>	adult	3	pinned
Carabidae	<i>Anisodactylus rusticus</i>	adult	3	pinned
Carabidae	<i>Anisodactylus sanctaecrucis</i>	adult	3	pinned
Carabidae	<i>Bembidion quadrimaculatum</i>	adult	3	pinned
Carabidae	<i>Bembidion rapidum</i>	adult	3	pinned
Carabidae	<i>Bembidion versicolor</i>	adult	3	pinned
Carabidae	<i>Bradycellus neglectus</i>	adult	1	pinned
Carabidae	<i>Bradycellus rupestris</i>	adult	3	pinned
Carabidae	<i>Calathus opaculus</i>	adult	3	pinned
Carabidae	<i>Chlaenius tomentosus</i>	adult	3	pinned
Carabidae	<i>Chlaenius tricolor</i>	adult	3	pinned
Carabidae	<i>Cicindelidia punctulata</i>	adult	3	pinned
Carabidae	<i>Cicindelidia sexguttata</i>	adult	3	pinned
Carabidae	<i>Clivina impressifrons</i>	adult	3	pinned
Carabidae	<i>Colliurius pensylvanica</i>	adult	1	pinned
Carabidae	<i>Cratacanthus dubius</i>	adult	3	pinned
Carabidae	<i>Cyclotrachelus sodalis</i>	adult	3	pinned
Carabidae	<i>Dyschirius globulosus</i>	adult	1	pinned
Carabidae	<i>Elaphropus anceps</i>	adult	3	pinned
Carabidae	<i>Galerita bicolor</i>	adult	2	pinned
Carabidae	<i>Harpalus affinis</i>	adult	3	pinned

Table 3.12. (cont'd)

Family	Genus-Species	Life Stage	Quantity	Preservation
Carabidae	<i>Harpalus amputatus</i>	adult	1	pinned
Carabidae	<i>Harpalus caliginosus</i>	adult	2	pinned
Carabidae	<i>Harpalus compar</i>	adult	3	pinned
Carabidae	<i>Harpalus herbivagus</i>	adult	3	pinned
Carabidae	<i>Harpalus pensylvanicus</i>	adult	3	pinned
Carabidae	<i>Harpalus rubripes</i>	adult	1	pinned
Carabidae	<i>Loricera pilicornis</i>	adult	3	pinned
Carabidae	<i>Notiophilus semistriatus</i>	adult	1	pinned
Carabidae	<i>Ophonus puncticeps</i>	adult	3	pinned
Carabidae	<i>Paraclivina bipustulata</i>	adult	3	pinned
Carabidae	<i>Poecilus chalcites</i>	adult	3	pinned
Carabidae	<i>Poecilus lucublandus</i>	adult	3	pinned
Carabidae	<i>Pterostichus melanarius</i>	adult	3	pinned
Carabidae	<i>Pterostichus obesulus</i>	adult	1	pinned
Carabidae	<i>Pterostichus permundus</i>	adult	3	pinned
Carabidae	<i>Scarites vicinus</i>	adult	3	pinned
Carabidae	<i>Stenolophus lecontei</i>	adult	1	pinned
Carabidae	<i>Stenolophus lineola</i>	adult	2	pinned
Carabidae	<i>Stenolophus ochropezus</i>	adult	3	pinned
Carabidae	<i>Stenolophus plebejus</i>	adult	2	pinned
Carabidae	<i>Stenolophus unknown</i>	adult	3	pinned

CHAPTER FOUR: PREDATION BY GROUND-DWELLING ARTHROPODS IN PRAIRIE STRIPS AND ADJACENT ROW CROPS

ABSTRACT

Agricultural intensification over the last century has resulted in habitat fragmentation and a loss in biodiversity and their associated ecosystem services. Conservation interventions in agriculture have the potential to support biodiversity through providing nesting and overwintering habitat and alternative prey or floral resources. Perennial prairie strips are a novel conservation practice that strategically places native prairie grasses and flowers within crops to reduce soil and nutrient runoff and provide habitat for biodiverse communities of pollinators and natural enemies. Prairie strips were introduced to two conservation-oriented treatments at the Kellogg Biological Station Long Term Ecological Research site in southwest, Michigan in 2019 and are the focus of this study. The treatments include Reduced Input, or one-third the conventional use of synthetic pesticides and fertilizers, and Biologically Based, or no synthetic inputs. In 2022, we placed sentinel insect pests and weed seeds within three exclosures types to study the question: what are the impacts of prairie strip establishment on predation service offered by natural predators both within the strip and adjacent row crop? Exclosures consisted of Open, Invertebrate-only, and Control and deployed a choice-experiment of either four sentinel insect pest species or four sentinel weed seeds common to the Midwest, US. Invertebrate predators accounted for ~ 50% of sentinel insect pest predation in both treatments, but Reduced Input had significantly higher overall predation rates by both invertebrates and vertebrates. By distance, predation rates of insect prey were highest either within the prairie strip or near to it, with a preference for larger sentinel prey. Overall, we observed low weed seed predation likely as a result of methodological errors; however, there was a slight preference for larger seeds, in particular giant Foxtail (*Setaria faberi* Hermm). In simplified agricultural landscapes, prairie strips are a valuable conservation practice to increase overall abundance and diversity of natural enemies and their associated predation services.

INTRODUCTION

Agricultural intensification over the last century has resulted in habitat fragmentation and a loss in biodiversity and their associated ecosystem services (Foley et al. 2005). Increased demands on producers has led to simplified landscapes dependent on high-input of synthetic

pesticides and fertilizers to maintain productivity. In light of the risk to biodiversity loss, “ecologically intensive” practices (Tiftonell 2014) have been promoted as an option to increase agricultural productivity through ecosystem service provision (Bommarco et al. 2013). Natural or semi-natural habitat (SNH) within agroecosystems supports the spillover of ecosystem services and exchange of populations across arable borders (Blitzer et al. 2012; Holland et al. 2016; Smith et al. 2014). Management practices that historically promoted tillage, pesticide use, and removal of SNH have resulted in the filtering of ecological communities (Gamez-Virues et al. 2015) to species with generalist feeding behavior dependent on disturbed agricultural landscapes capable of quickly recolonizing disturbed habitats (Blitzer et al. 2012). Conservation interventions that support habitat diversity may then support the diversity of service-providing organisms in agricultural landscapes.

A meta-analysis by Martin et al. (2019), found that increasing habitat diversity and configuration within agricultural landscapes increased pollination by 1.7-fold and pest control by 1.4-fold; however, the benefits can be taxa specific and dependent on broader landscape composition. Martin et al. (2019) further found that landscapes with SNH < 5% benefited the least from increased edge density, likely due to a lack of source populations. In highly diverse agroecosystems with SNH > 50%, population spillover is already likely and does not benefit from conservation interventions, especially for organisms with low dispersal abilities (Smith et al. 2014; Beaumelle et al. 2021). This supports the intermediate landscape-complexity hypothesis introduced by Tscharrntke et al. (2012) and provides evidence for strategic placement of conservation interventions.

Increased landscape diversification increases necessary habitat and alternative resources for beneficial organisms, such as natural predators, that are particularly important to growers. Many arthropods provide natural pest suppression, including parasitoids and predators of egg, larval or adult stages throughout the growing season. Natural enemies also feed on pest species at different life stages, such as the green lacewing that predate on aphids as larvae and nectar or pollen as an adult (Gonzales et al. 2024). Conservation interventions that diversify agricultural landscapes provide alternative habitat to support natural enemy overwintering, nesting behavior, and prey sources (Haan et al. 2021; Landis 2000; Tscharrntke et al. 2005; Bianchi et al. 2006; Rusch et al. 2010). In their study on green lacewings, Gonzales et al. (2024) found that increasing the floral availability near crops encouraged the lacewings to fly shorter distances,

particularly during early season when predation services are most valuable for the suppression of pest populations. Ground-dwelling arthropods are also highly valuable natural enemies in agricultural landscapes that may benefit from conservation interventions. In European agroecosystems, beetle banks have long been used to encourage populations of carabids (Thomas et al. 1991; MacLeod et al. 2004), which predate both insect pests and weed seeds (Kulkarni et al. 2015, other sources). In the Midwest, US, flower strips and grasslands have also been studied to support local populations of ants (Wills et al. 2019; Helms et al. 2021) and spiders (Cox et al. 2014; Campbell et al. 2020). Spiders are dependent on plant litter for both overwintering and hunting (Clem and Threatt 2021), while carabid overwintering abundance and diversity increased in SNH placed near spring-sown crops (Bannwart et al. 2025), likely as a result of protection from soil disturbance caused by spring tillage.

Perennial prairie strips or plantings are a novel conservation intervention introduced by researchers at Iowa State University to reduce agricultural runoff and provide non-crop habitat for biodiversity conservation and ecosystem service provision (Schulte et al. 2017). Prairie strips provide a diversity of native flowers and grasses to support beneficial arthropod populations; in Iowa, strips resulted in 3.5-fold increase in pollination and 2.6-fold increase in overall taxa richness. In 2019, prairie strips were placed in two conservation-oriented treatments at the Kellogg Biological Station (KBS) Long Term Ecological Research Main Cropping Systems Treatment (LTER MCSE) in southwest Michigan and provided an opportunity to study how prairie strips affected beneficial arthropod populations and their services. The LTER MCSE prairie strips have been shown to increase the abundance and diversity of butterfly (Kemmerling et al. 2023), dung beetle (Kemmerling et al. 2022), and ground beetle (Fiser et al. 2025 *in prep*) populations. We also know that long-term agricultural management can influence the composition of arthropod communities, such as carabids (Fiser et al. 2025), and carabid communities differ in their response to prairie strips based on in-field management practices (Fiser et al. 2025 *in prep*).

To address the gap in knowledge on predation services provided by the establishment of prairie strips, we hypothesized that a) strips would result in the spillover of predation services in the adjacent row crop; and b) that overall predation would differ by in-field management practices.

METHODS AND MATERIALS

Study Site

This study took place at the Kellogg Biological Station (KBS), Long-term Ecological Research site (LTER), Main Cropping Stems Experiment (MCSE) in Hickory Corners, Michigan (42.411078, -85.377195). The MCSE is a randomized complete block experiment, comprised of seven treatments along a gradient of low-high agricultural intensity, including annual and perennial cropping systems. Treatments are replicated six times in 0.88-hectare plots (87m x 105m) (Figure 4.1.A). Annual crop treatments in the KBS-LTER reflect practices used in the surrounding southwest Michigan region, including a corn-soybean-wheat rotation with corn and soybean planted May-June and harvested in the fall, and wheat planted in July and harvested the following year (Robertson and Hamilton 2015). The KBS-LTER employs cover crops in all annual crop treatments, with red clover (*Trifolium pratense* L.) planted after wheat harvest, and cereal rye (*Secale cereale* L.) planted after corn harvest.

This study took place in the two ‘conservation-oriented’ annual crop treatments, Reduced Input and Biologically Based. The Reduced Input treatment has one-third the input of conventional row crops, and the Biologically Based treatment has zero synthetic inputs (Table 4.5). A pre-emergence herbicide is applied to Reduced Input, and both treatments are rotary-hoed for weed management; prior to cover crop seeding, both treatments are also chisel-plowed and soil finished.

The KBS-LTER periodically adjusts agricultural management based on current practices or pest outbreak; however, management goals have largely remained the same since the LTER was established in 1989. Full application details can be found in the agronomic log available at the KBS-LTER website (kbs.lter.msu.edu).

Prairie Strips

Perennial prairie strips were planted in April 2019 in all replicates of the Reduced Input and Biologically Based treatments, bisecting each replicate with 5m wide x 105m long strips (Figure 4.1.B). The perennial seed mix included a mixture of four cool and warm season grass species and 18 forb species which provide floral resources throughout the growing season (Table 4.4). To assist with establishment in the first year, a nurse crop of annual oat and rye were mixed into the initial seeding; the strip is then burned each subsequent spring to reduce invasion of woody vegetation.

Predation Sampling

We evaluated predation of sentinel insect pests and weed seeds within prairie strips and adjacent crop fields. As detailed in Helms et al. (2021) three transects were placed perpendicular to the prairie strip in each replicate and extended to field center. To reduce edge effects, all sampling stations were at least 20m from the field perimeter. Sampling stations were established at 0m (within strip center), and 1, 5, and 20 m into the row crop. Transects were rotated weekly to avoid oversampling any area of the plot or baiting predators to certain locales, with no sampling occurring during the fourth week.

At each sampling station sentinel prey were displayed on cards with different levels of predator enclosure. Prey cards were made from 3M aluminum oxide 80-grit tan sandpaper that mimics the texture and color of the soil surface. Each sentinel insect prey or seed species was affixed to the cards using 3M 77 clear spray adhesive. Predation cards were secured in place using metal ground staples under one of three enclosure levels (Figure 4.2). Control enclosures were inaccessible to all predators, Invertebrate-only enclosures limited predation to small arthropods, and Open consisted of no enclosure with prey accessible to all potential predators including birds, mammals, and arthropods. The Invertebrate-only and Control enclosures consisted of 1.25 cm hardware mesh cages (13 cm long x 10 cm wide x 10 cm tall) placed over sentinel prey cards and secured with metal ground staples. In the Control enclosures, prey cards were further enclosed within a micrometer mesh bag to prevent all potential predation and to measure any loss of prey due to handling (per Gaines-Day and Gratton 2010).

At each sampling station, Open and Invertebrate-only enclosures were placed 1 m apart. Predation cards were placed out for 48 h and collected in sequential order, placed within a plastic bag to prevent loss of material in transport to the lab, and placed in a standard freezer at -18 C until later analysis. Control enclosures were placed in one randomly selected replicate of each treatment each sampling week and placed at both the 0 m and 20 m sampling locations (prairie strip or field center). The study displayed prey in a choice design, with all four species of insect or weed seed placed on the cards in a 4 x 4 grid pattern with one prey species per grid (Figure 4.3).

Sentinel Pest Insect Predation Experiment

To test for predation of common pest insects we used sentinel prey in either the larval or pupal form, frozen at -18 C for at least one week prior to placement in the field. The sentinel

insects included pupae of European corn borer (*Ostrinia nubilalis* Hübner), greater waxworm (*Galleria mellonella* Linnaeus) larvae, house fly (*Musca domestica* Linnaeus) pupae, and fruit fly (flightless *Drosophila melanogaster*) pupae. Overall prey volume was controlled by size using three European corn borer pupae, three waxworm larvae, five house fly pupae, and 10 fruit fly pupae and secured on the card using the spray adhesive. European corn borer pupae were supplied by the USDA ARS Corn Insects and Crop Genetics research unit at Ames, IA. The remaining insect prey were bought from a local pet feed supplier and immediately frozen. Insect prey were counted as “attacked” if an individual was completely removed or had visual signs of wounding. All samples were placed for 48h; however, each sample was visited after 24 h and if all sentinel prey were removed the card was then collected with a note on the time.

Sentinel Weed Seed Predation

To test for predation of common agricultural weed seeds, we used four species varying in size and shape. These included velvetleaf (*Abutilon theophrasti* Medik), common lambsquarters (*Chenopodium giganteum*), pigweed (*Amaranthus* sp.), and giant foxtail (*Setaria faberi* Hermm). The species used in this study were selected for their known herbicide resistance in the Midwest (although not specifically at the KBS-LTER site) (Menalled et al. 2000; *MSU extension resources*) which makes them difficult to control. Seeds were purchased from Azlin Seed Service (Leland, Mississippi). All seeds were steam sterilized to kill them prior to placement in the field. This was completed using an autoclave at 100 C and 1 kg/cm² pressure for one hour (per Appanah 1987). Per predation card, nine seeds from each species were placed in each quadrant using spray adhesive. Weed seed predation was counted as “attacked” if a seed was removed from the card.

Statistical Analysis

Overall, there were 1440 sentinel insect cards and 1440 weed seed cards placed from May – September 2022 (2 treatments x 6 replicates x 5 months x 3 transects x 4 sampling stations/transect x 2 enclosure types). When accounting for the choice experiment, predation was determined by measuring the overall predation rate per species across all sampling events (not by individual cards) and averaged by each variable (enclosure type, treatment, month, and distance) (Figure 4.S4). We used the R package *lme4* (Bates et al. 2015) to test for differences in overall predation rates by treatment, month, distance, and enclosure type by pooling 12 samples across 3 transects for one sampling period per month. We used Generalized Linear Models (GLMs) with

a negative binomial distribution to test multiple variables for insect and weed seed predation, including treatment (Reduced Input vs. Biologically Based), growing season (May – September), distance from prairie strip (0, 1, 5, and 20 m from strip edge), and sentinel species; replicate was used as a random effect. We determined the best fit model using QAICc and post-hoc pairwise tests for significant pairwise differences in the best fit model using the “emmeans” function in the R package *emmeans* (Lenth et al. 2023).

RESULTS

Sentinel Insect Predation

Overall, insect prey experienced high rates of predation in this experiment with median proportion consumed reaching 1.0 in the Open exclosures where both vertebrates and invertebrates had access to the sentinel prey, and 0.0-0.7 consumed in the Invertebrate-only exclosures (Figure 4.6). There was generally very low predation in Control exclosures, however there were a few instances where predators penetrated them, typically evidenced by chewing marks on the mesh bags. Since the focus of the study was on invertebrate predation, hereafter we focus on those results.

In the Invertebrate-only exclosures, predation of sentinel insect prey exhibited a distinctly bimodal pattern (Figure 4.7). Many cards experienced no predation, generally low numbers of cards with intermediate levels of predation, and large number of cards experiencing a high proportion of prey removed. Mean proportion of sentinel prey consumed was $0.57 (\pm 0.01)$, while the median prey consumed was 0.9, indicating more instances of high predation (Table 4.1.A). Treatment was a significant factor in overall predation of insect prey ($f = 19.48$; $p < 0.001$) (Figure 4.7), as was month ($f = 27.04$; $p < 0.001$) (Figure 4.8), and distance from prairie strip ($f = 40.15$; $p < 0.001$) (Figure 4.9). Although the best fit model (Table 2) included all three variables, only the interaction between treatment and month was significant ($f = 27.04$; $p < 0.001$) and not treatment and distance ($f = 1.94$; $p > 0.05$). Predation was higher in the prairie strip (0 m) than 1, 5, and 20 m into the row crop for both treatments (Table 4.1.B) (Figure 4.9), although predation in Reduced Input within the prairie strip was higher than Biologically Based (0.69 ± 0.02 vs. 0.58 ± 0.02 proportion prey consumed). Pest insect predation also varied by treatment and month, with overall higher predation in June (0.62 ± 0.02) and July (0.6 ± 0.02) compared to early and late season (Table 4.1.C) (Figure 4.8). The Reduced Input treatment had higher predation rates at two points during the growing season in June (0.68 ± 0.02) and

September (0.62 ± 0.02), whereas Biologically Based peaked mid-season in June-July (0.6 ± 0.02).

Individual sentinel insect species had variable predation rates, particularly in respect to distance from prairie strip. Larger sentinel prey, European corn borer pupae and waxworm larvae, had higher overall predation rates compared to the smaller house fly and fruit fly pupae (Figure 4.10). Larger prey continued to exhibit higher predation rates (median = 100% consumed for both), while the smaller prey both had decreasing predation with increased distance from the prairie strip (Figure 4.11). In particular, house fly pupae had the lowest median predation rate at 20m into the field compared to fruit fly pupae.

This study focused on invertebrate predators; however, we also included Open exclosures to determine overall predation rate including all predators (rodents and small mammals, birds, etc.). The Open exclosures had overall higher predation rates than Invertebrate-only (0.72 ± 0.01 vs. 0.57 ± 0.01) (Table 4.6.A). Similar to the patterns observed in Invertebrate-only exclosures, predation was higher in the Reduced Input than Biologically Based (0.77 ± 0.01 vs. 0.69 ± 0.02). By distance, predation remained high in the Open exclosures throughout the field but was highest in the prairie strip (Table 4.6.B).

All predation cards for all exclosures were placed in the morning and collected in sequential order after 48 h (24 h if the entire card was observed to be predated). On several conditions, the sentinel insect prey cards (both Open and Invertebrate-only) were entirely consumed < 12 h after placement (field observations). Data were also collected throughout the length of this study on predators observed to actively use the predation cards 24 h after placement. Most common predator genera included: Formicidae (ants), Opilionidae (harvestmen), and Aranea (spiders) on both Open and Invertebrate-only, while Rodentia was observed most often (via fecal matter observed on cards) on the Open cards. (Figure 4.5).

Sentinel Weed Seed Predation

In contrast to the high rates of insect predation reported above, weed seeds experienced little to no predation in this experiment. (Figure 4.12) (Table 4.3) which was likely a result of the way we evaluated predation. We considered a seed attacked only if it was fully removed from the card, but in retrospect, the strength of the adhesive spray may have limited the ability of granivores to remove seeds. In a subsequent experiment using this method we observed scratch marks on some seeds suggesting unsuccessful attempts at removal. Due to the low removal rates

of weed seeds, statistical models overestimate potential interactions between different variables. However, there is limited evidence that larger seeds (foxtail and velvetleaf) were more often removed at higher rates than smaller seeds (Figure 4.12, 4.13). Foxtail seeds have softer seed coatings and are considered more palatable, and when exposed on the soil surface, are preferred by a variety of predators including rodents and birds (Moehler et al. 2021). Foxtail also had slightly higher predation at field center compared to the prairie strip (Figure 4.13).

DISCUSSION

Our study demonstrated that invertebrate predators account for ~50% of sentinel insect pest predation in row crop agriculture. The introduction of perennial prairie strips to two conservation-oriented treatments at the KBS-LTER resulted in increased predation rates both within and near to the strip with limited spillover to the field center. In addition, mature prairie strips provide valuable refuge during early season and post-harvest when few resources are available in the surrounding row crops.

Sentinel Insect Pest Predation

Ground-dwelling arthropods provide valuable pest suppression in agricultural fields. Arthropods provided an average of ~ 50% predation in both conservation-oriented treatments; while the conventional Reduced Input treatment had slightly higher predation compared to the Biologically Based treatment. This result was initially surprising as organic treatments are typically host to more diverse natural enemy communities throughout the growing season (Fiser et al. 2025; Helms et al. 2021), but we did not observe this pattern. In their study within orchards, Galloway et al. (2021) found that native predators were more abundant and species rich in organic treatments; however, they also found that predator abundance and species diversity were greater in conventional treatments with introduced SNH than conventional treatments alone. The introduction of prairie strips may have been more beneficial to the Reduced Input treatment than Biologically Based, which does not receive synthetic inputs and has historically higher weed prevalence.

Across treatments, predation rates were highest within or near-to the prairie strips, likely a result of alternative prey or floral resources, protection from disturbance, and the vegetative cover strips provide. We observed multiple predators in both the prairie strip and row crop, including spiders (Aranea), harvestmen (Opilionidae), ants (Formicidae), and carabids (Carabidae) among others. In studies on SNH in agricultural landscapes, spiders have been found

75% of the time in perennial SNH cover compared to adjacent wheat crops (Schmidt and Tscharntke 2005b), particularly during early spring (Schmidt and Tscharntke 2005a; Keswani 2023) especially for web-building species like Linyphiidae or Thomisidae. Harvestmen are less studied than other dominant arthropod predators but have also been found to positively respond to conservation interventions. In their study on grapeberry moths in vineyards, Papura et al. (2020) found that harvestmen had higher predation rates in vineyards with increased proportions of SNH in the surrounding landscape and was not solely a response to increased alternative prey.

Ants and carabids are well-known and diverse predators of both insects and weed seeds in agricultural landscapes. In our study, we observed ants at higher numbers and on more predation cards than any other predator (field observations). In previous studies conducted at the KBS-LTER, Helms et al. (2021) found that the Reduced Input treatment had higher overall ant activity, but 75% occurred after fall harvest, in contrast, the Biologically Based treatment had consistent ant foraging activity throughout the growing season. Other studies conducted at KBS found that perennial systems had increased ant abundance and species rich communities compared to annual systems, in particular, annual row crops (Haan et al. 2024). Ground beetle communities vary by treatment but increase in both diversity and richness with the introduction of prairie strips (Fiser et al. 2025, Fiser et al. 2025 *in prep*). The literature predominantly supports carabids as beneficial predators in agriculture, consuming insect prey and weed seeds (Kulkarni et al. 2015), and contributing to overall pest predation. However, the authors note that several studies show varied results of carabid pest predation (Vargas 2024) or potential disservices (Botezl and Knapp 2024).

Sentinel Pest Insect Choice-Experiment

We observed high predation of sentinel insect pests across treatments both within the prairie strip and row crop; however, predation varied by pest species. The sentinel insect pest species were selected for their differences in size and accessibility (soft or hard pupal shell vs. larvae) as a choice experiment. European corn borer and greater waxworm had overall high predation rates at all distances from the prairie strip, however, the smaller house fly and fruit fly pupae reduced in predation with distance from the prairie strip. One hypothesis is that higher abundance of predators either within or nearby the prairie strip resulted in higher predation of all species on the sample card. Another hypothesis is the diversity in carabid species size in the prairie strip and prey preference. The exterior hardness of the pupal shell did not change the

predation rate, as both the corn borer pupae and soft waxworm had similar predation rates. At distances further from the prairie strip where fruit fly and house fly predation rates are lowest, arthropods may be exhibiting predator avoidance behavior. Insect risk behavior in agriculture is not well-studied, however, a laboratory experiment found that insects facing predation risk are less ‘choosy’ towards available resources. The less ‘choosy’ individuals tended to consume more rather than less resources (Charalabidis et al. 2017). Because higher predation was not observed at field center in our study and our choice-experiment showed a preference for larger prey, future studies should look into predator avoidance behavior in arable crops compared to perennial prairie strips.

Method Accuracy and Limitations

The authors understand potential limitations presented in this study. Predation cards were placed in the morning and collected after 48 h in sequential order; however, many of the Open and Invertebrate-only cards had 100% predation after <12h. In this scenario, it is likely that we overestimated the predation potential of diurnal species such as spiders and ants, and underestimated the nocturnal species, such as carabids. Future studies should consider placing 12 h traps both during the day and the evening to measure both forms of predation. Furthermore, we were unable to say exactly what invertebrate predators consumed the sentinel insect prey outside of few observations during the day. Although we know the predators were small arthropods using the Invertebrate-only enclosure, it would be beneficial to know what predators are most prevalent and gear interventions to better support their pest suppression services. Using field cameras or conducting an analysis of the gut of common arthropod predators may provide this information. Lastly, we were unable to collect accurate data on weed seed predation due to methodological error; seed removal may have been prevented due to the adhesive spray used and predation may have occurred on a smaller scale than was looked for.

CONCLUSIONS

In simplified agricultural landscapes, prairie strips are a valuable conservation practice to increase overall abundance and diversity of natural enemies and their associated predation services. Our study found that field-level management practices significantly impacted the predation level of sentinel insect pests after prairie strip establishment. This result is corroborated by the literature on increased value of SNH in landscapes surrounding conventional row crop management. We also found that prairie strips increased overall predation by invertebrates and

vertebrate predators near-to the prairie strip, and that pest predation within the field may be pest species-specific. Many native invertebrate predators were also observed both within the strip and adjacent row crop that are known to benefit from increased SNH in the landscape. These results suggest that strategic use of conservation interventions, such as prairie strips, may provide valuable pest predation services for farmers and that ecosystem service provision requires both a field and landscape scale approach.

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APPENDIX. CHAPTER FOUR FIGURES AND TABLES

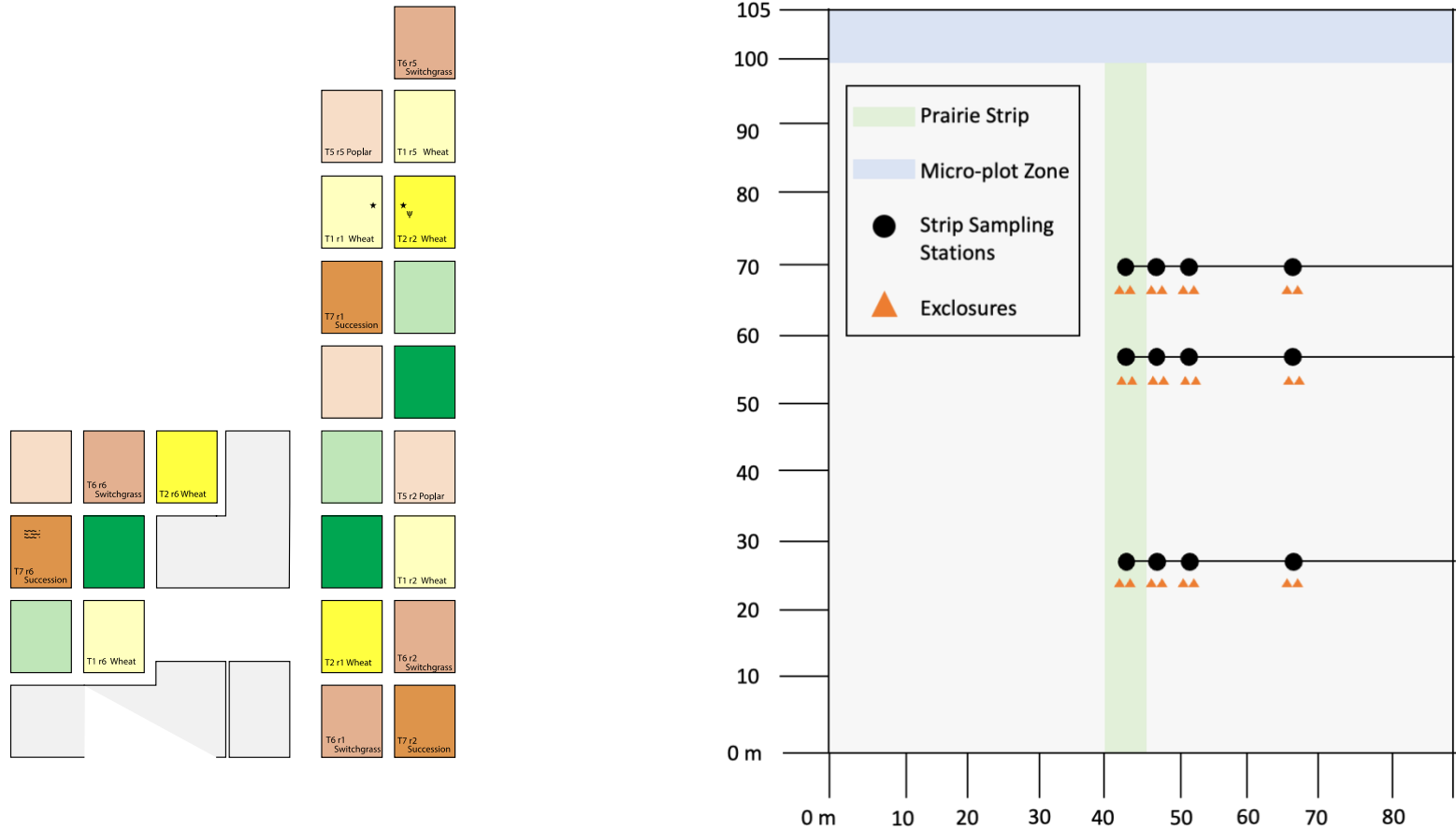


Figure 4.1. A) Kellogg Biological Station (KBS) Long-term Ecological Research (LTER) Main Cropping Systems Experiment 2022 and B) Plot-Level Experimental Design for the Reduced Input and Biologically Based treatments at the KBS-LTER MCSE in Hickory Corners, MI.

A.



B.

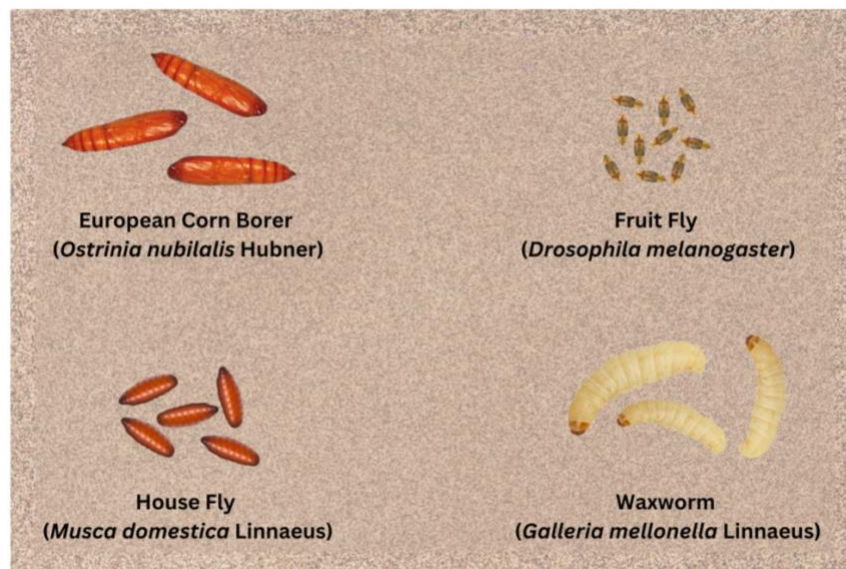


C.



Figure 4.2. Pictures of enclosure types used in 2022 predation experiment for both sentinel pest insects and weed seeds. A) Control or fully closed enclosure in wheat field; B) Invertebrate-only enclosure in prairie strip; and C) Open the KBS-LTER MCSE in Hickory Corners, MI.

A)



B)

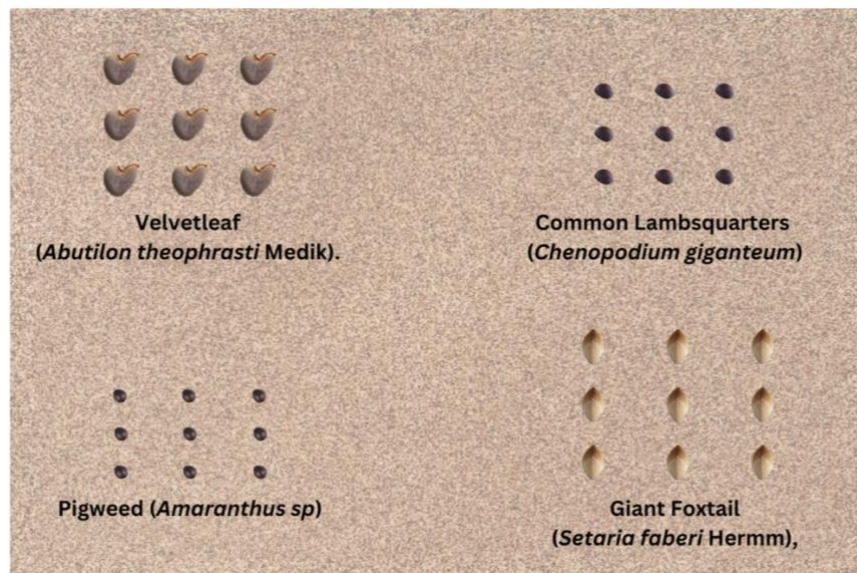


Figure 4.3. Graphic depiction of prey cards used in the 2022 predation experiments including A) Sentinel pest insect predation card with European corn borer (*Ostrinia nubilalis* Hübner), fruit fly (*Drosophila melanogaster*), house fly (*Musca domestica* Linnaeus), and greater waxworm (*Galleria mellonella* Linnaeus); and B) Weed seed predation cards with giant foxtail (*Setaria faberi* Hermm), common lambsquarters (*Chenopodium giganteum*), pigweed (*Amaranthus* sp), and velvetleaf (*Abutilon theophrasti* Medik). KBS-LTER MCSE in Hickory Corners, MI.

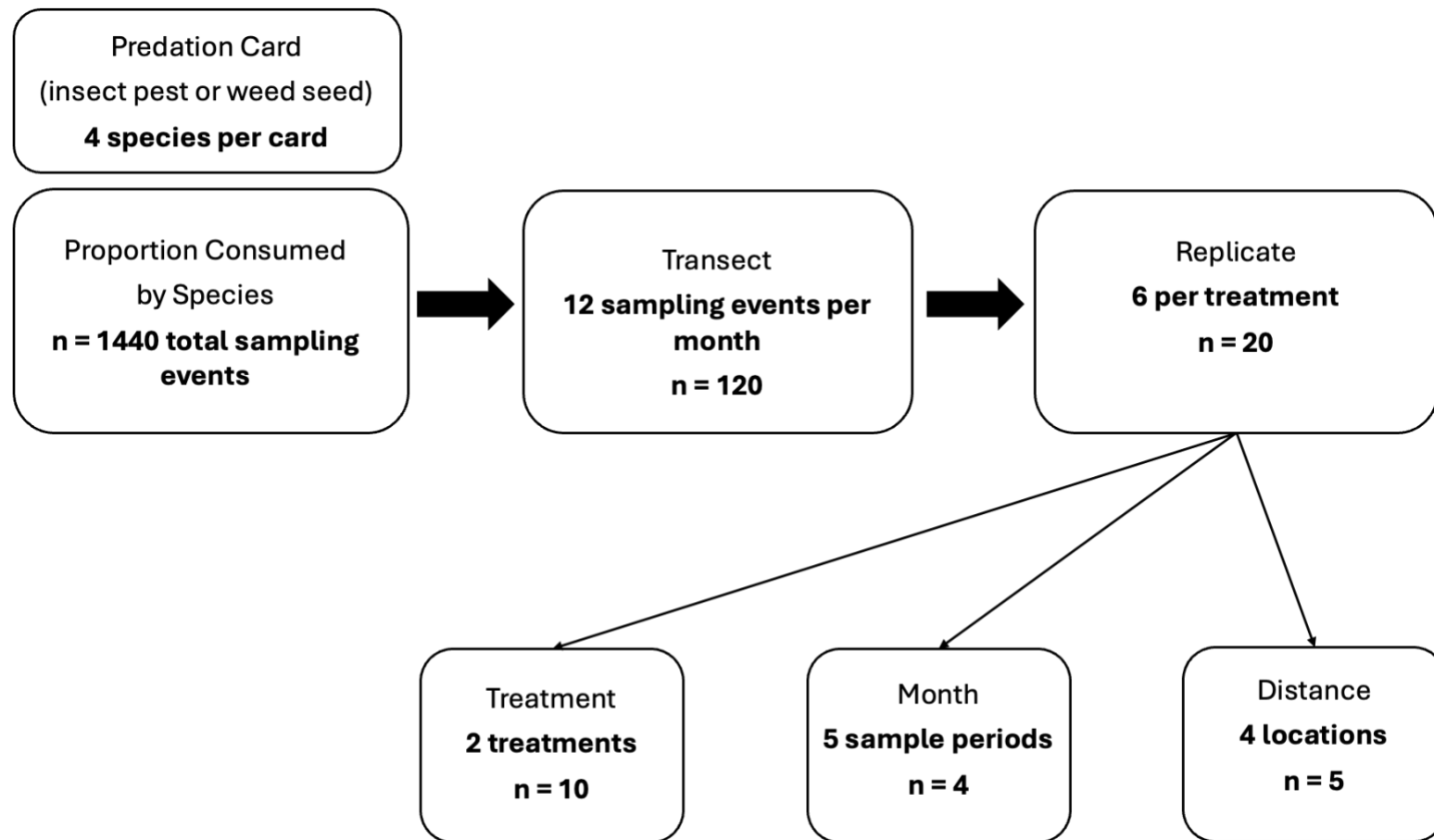


Figure 4.4. Predation cards (both sentinel insect prey or weed seeds) were prepared as a choice experiment with four species per quadrant of each card and predation was recorded as proportion consumed (ratio) for each species per sampling event (*not* per card) in 2022; we then took the average proportion consumed by species pooled across transects or 12 samples per sampling period (month) for each replicate. Lastly, we took the average proportion consumed of each species by replicate and totaled it for the variable used, listed as treatment (Reduced Input vs. Biologically Based), Month (May-Sept), or distance (0, 1, 5, and 20m from prairie strip edge).

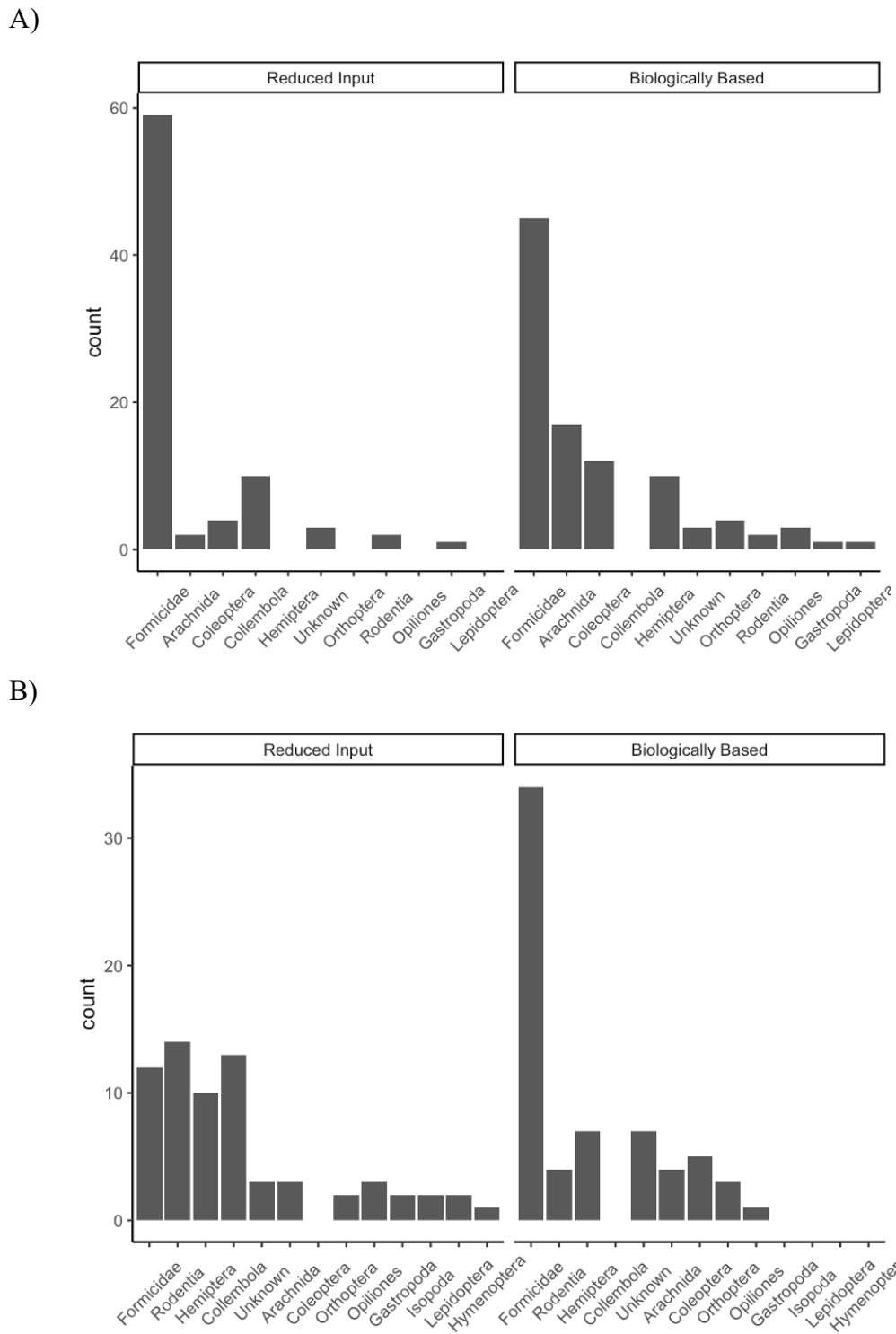


Figure 4.5. Arthropod predators observed to actively use the sentinel insect prey cards 24h after placement in A) Invertebrate-only enclosure; and B) open for 2022. Most common predator order included: Formicidae (ants), Opilionidae (harvestman), Aranea (spiders), and Rodentia (mice, ground-squirrels, etc.). KBS-LTER MCSE in Hickory Corners, MI.

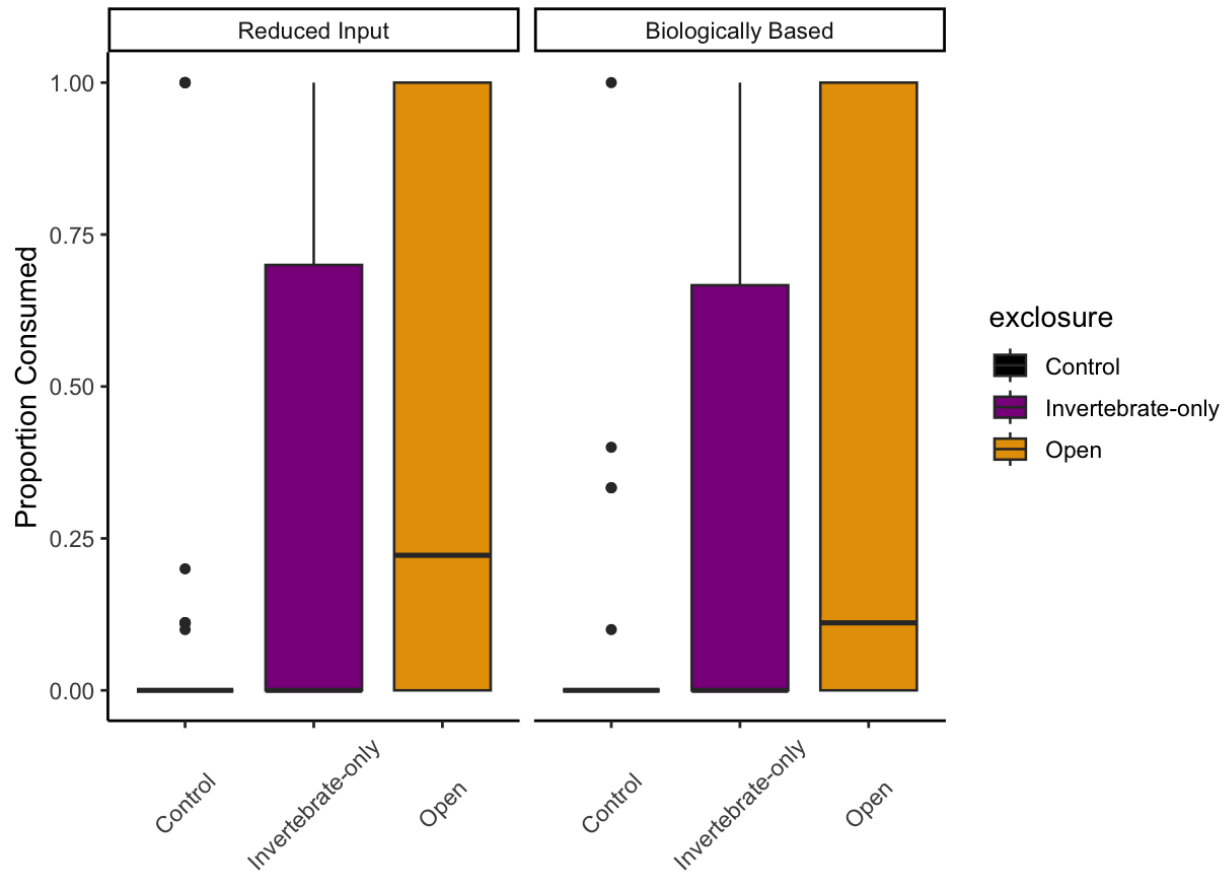


Figure 4.6. Proportion of sentinel insect pest species consumed in Reduced Input vs. Biologically Based treatments by enclosure type across all distances and sampling periods in 2022 at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI. Control enclosures were inaccessible to all predators, Invertebrate-only enclosures limited predation to arthropods, and Open consisted of no enclosure with prey accessible to all potential predators including birds, mammals, and arthropods.

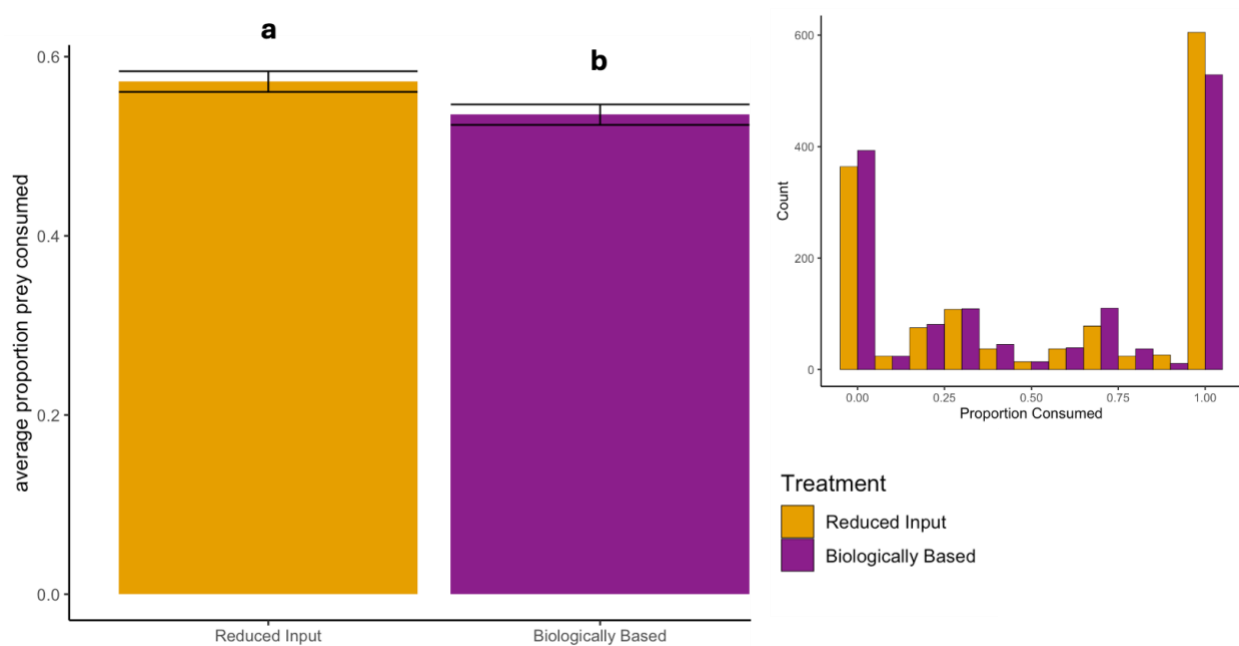


Figure 4.7. Proportion consumed (subset, right with range 0-1 by count) and mean \pm SE proportion consumed (left) of all sentinel insect pest species in 2022 by treatment (Reduced Input vs. Biologically Based) using ANOVA pairwise tests ($f = 19.48$; $p < 0.001$). Averaged across all distances and the entire growing season at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

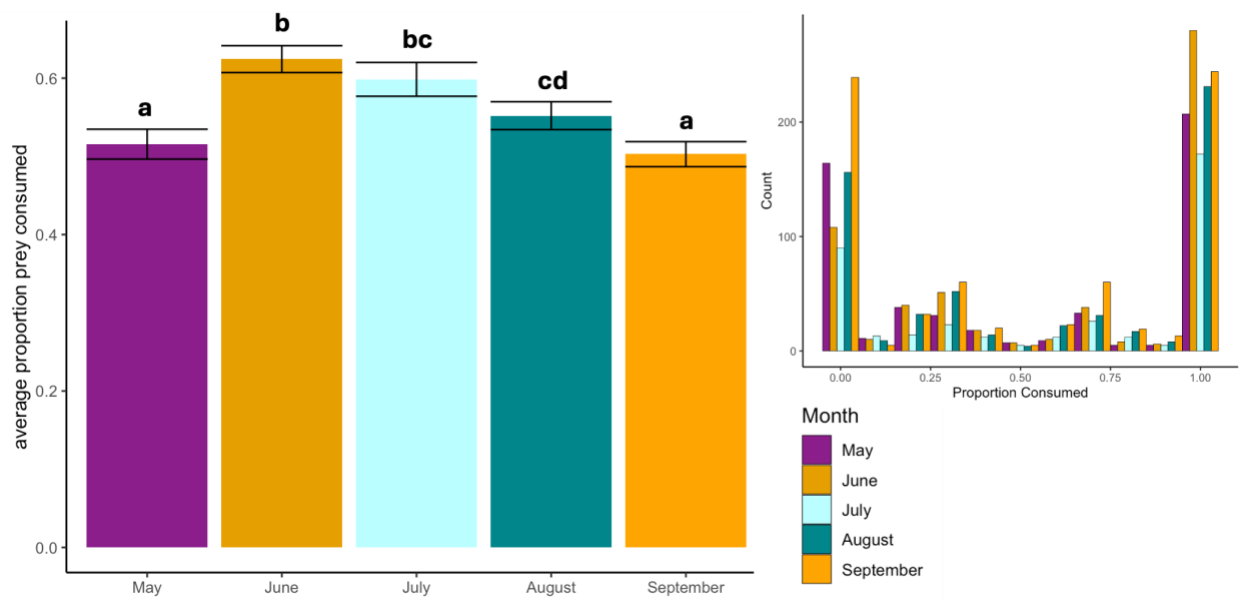


Figure 4.8. Proportion consumed (subset, right with range 0-1 by count) and mean \pm SE proportion consumed (left) of all sentinel insect pest species in 2022 by month during the growing season (May- September) using ANOVA pairwise tests ($f = 27.04$; $p < 0.001$). Averaged across both treatments and all distances at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

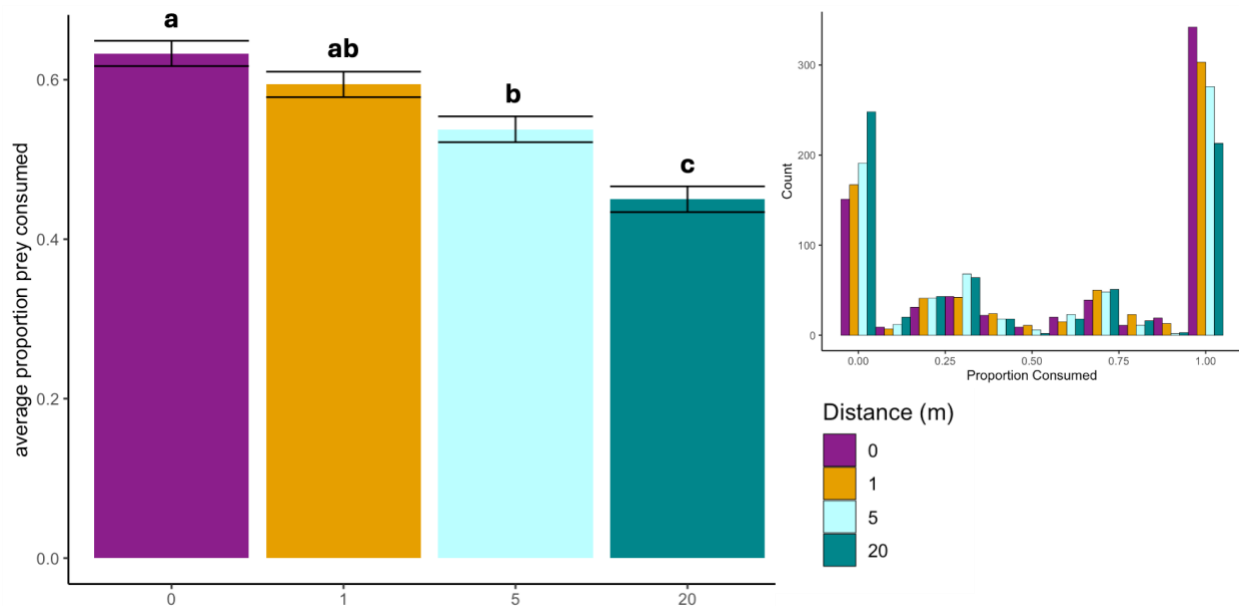


Figure 4.9. Proportion consumed (subset, right with range 0-1 by count) and mean \pm SE proportion consumed (left) of all sentinel insect pest species in 2022 by distance from prairie strip, including 0m (within strip), 1, 5, and 20m into the adjacent field crop using ANOVA pairwise tests ($f = 40.15$; $p < 0.001$). Averaged across both treatments and the entire growing season at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

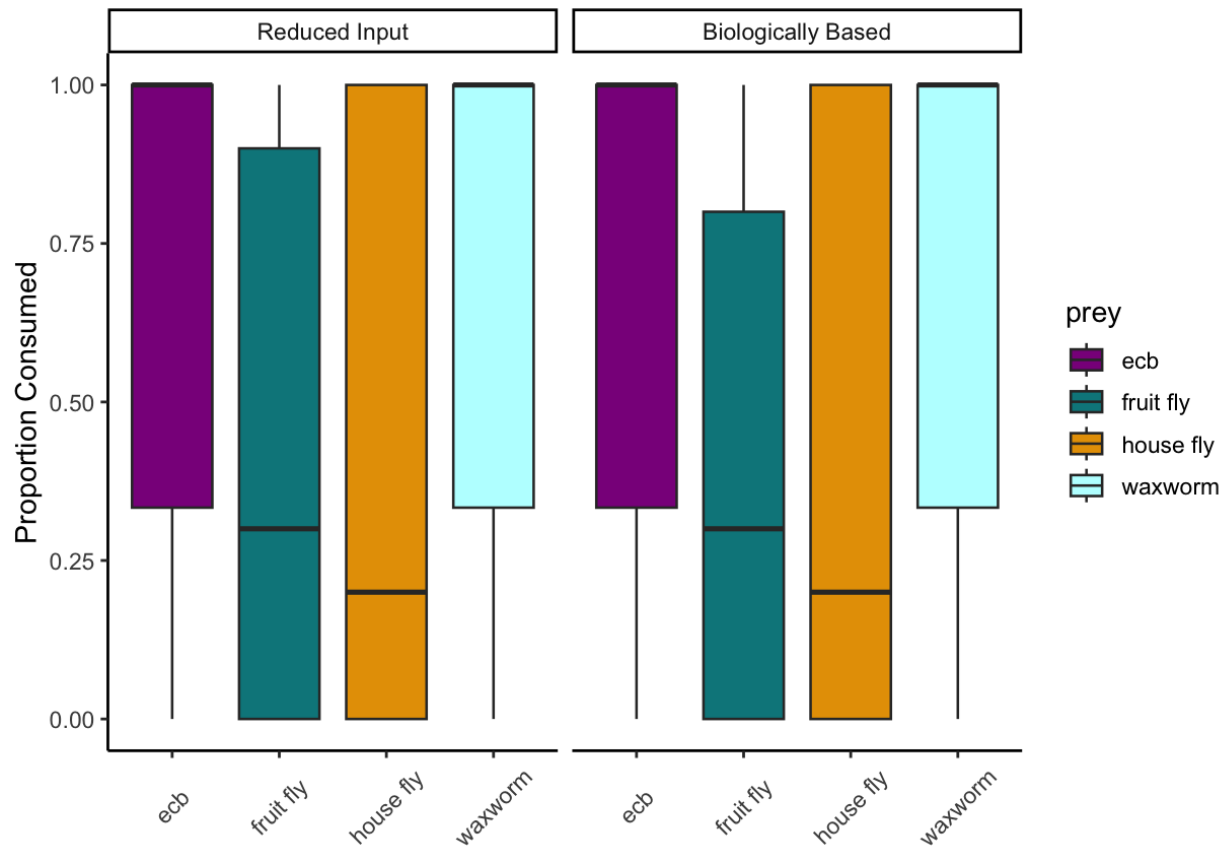


Figure 4.10. Proportion consumed (range 0-1) of sentinel insect pest species in 2022 from the Invertebrate-only enclosure, including the European corn borer (*Ostrinia nubilalis* Hübner), fruit fly (*Drosophila melanogaster*), house fly (*Musca domestica* Linnaeus), and greater waxworm (*Galleria mellonella* Linnaeus) by treatment (Reduced Input vs. Biologically Based) and across all distances and the entire growing season at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

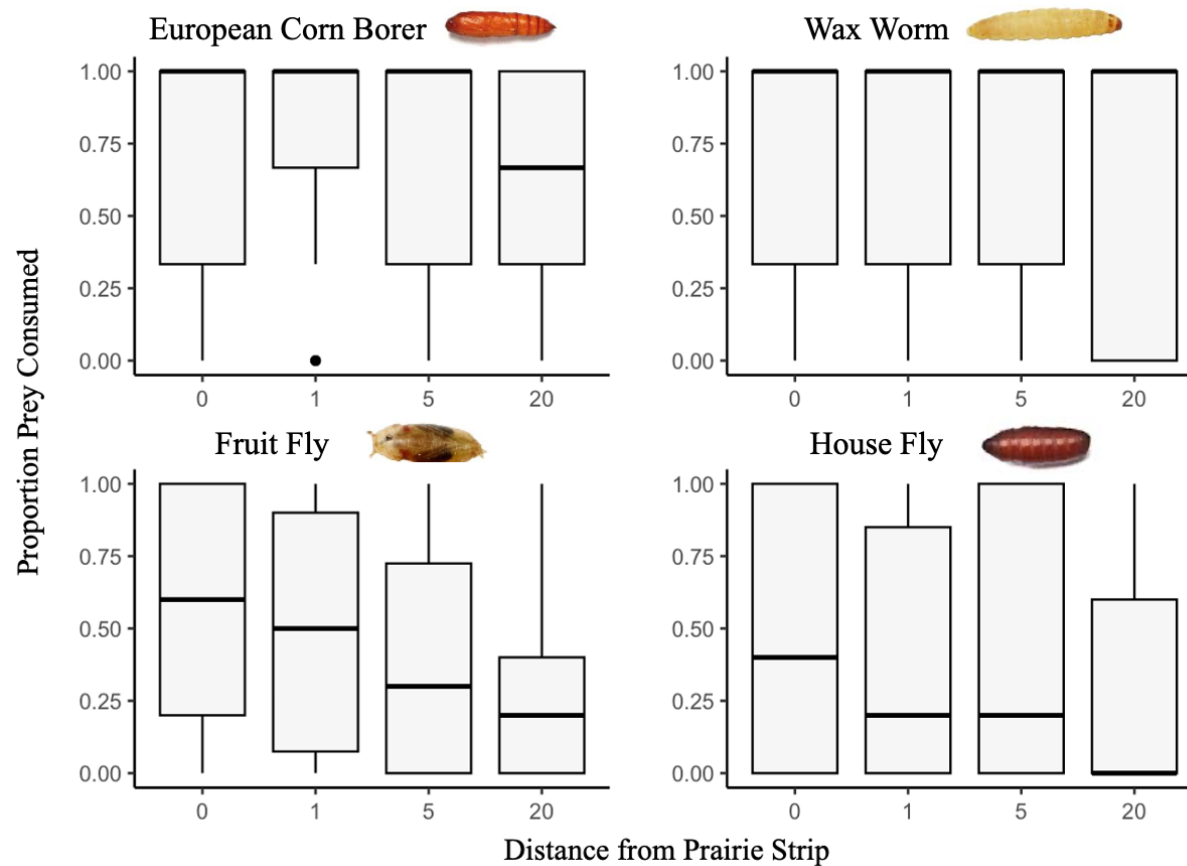


Figure 4.11. Proportion consumed (0-1) of sentinel insect pest species in 2022 from the Invertebrate-only enclosure, including the European corn borer (*Ostrinia nubilalis* Hübner), fruit fly (*Drosophila melanogaster*), house fly (*Musca domestica* Linnaeus), and greater waxworm (*Galleria mellonella* Linnaeus) by distance from prairie strip, including 0m (within strip), 1, 5, and 20m into the adjacent field crop for the entire growing season and for both the Reduced Input and Biologically Based treatments at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

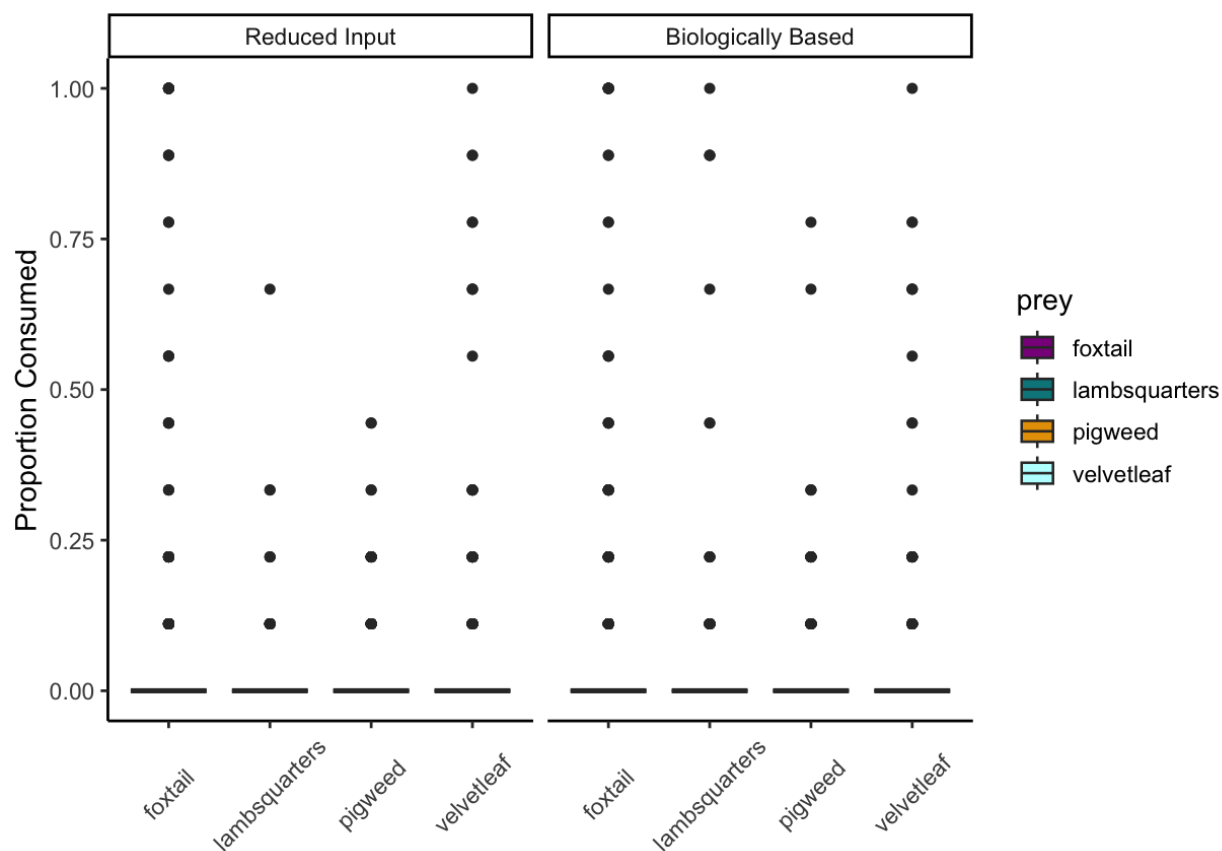


Figure 4.12. Proportion consumed (0-1) of sentinel weed seeds in 2022 from the Invertebrate-only enclosure, including giant foxtail (*Setaria faberi* Hermm), common lambsquarters (*Chenopodium giganteum*), pigweed (*Amaranthus sp*), and velvetleaf (*Abutilon theophrasti* Medik) by treatment (Reduced Input vs. Biologically Based) and across all distances and the entire growing season at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

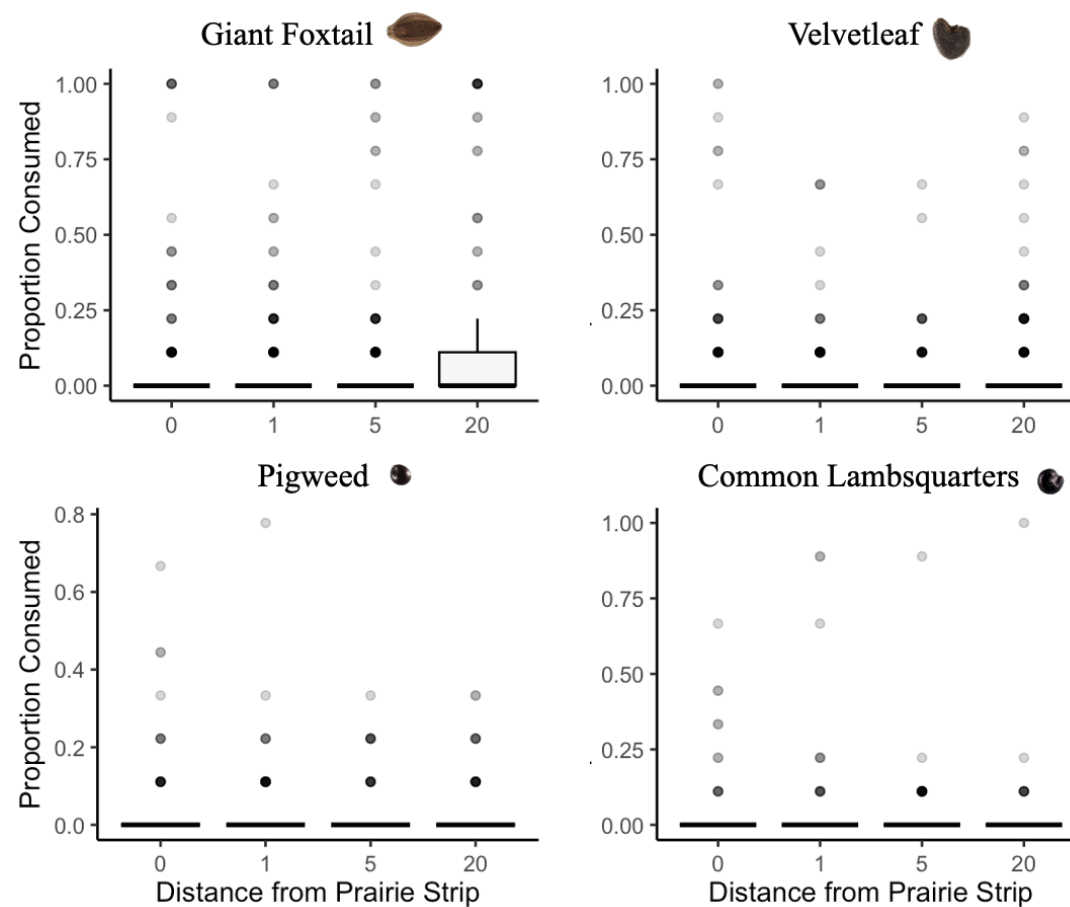


Figure 4.13. Proportion consumed (0-1) of weed seed species in 2022 from the Invertebrate-only enclosure, including the giant foxtail (*Setaria faberi* Hermm), common lambsquarters (*Chenopodium giganteum*), pigweed (*Amaranthus sp*), and velvetleaf (*Abutilon theophrasti* Medik) by distance from prairie strip, including 0m (within strip), 1, 5, and 20m into the adjacent field crop for the entire growing season and for both the Reduced Input and Biologically Based treatments at the KBS-LTER Main Cropping Systems Experiment, Hickory Corners MI.

Table 4.1. Mean and standard error (SE) for proportion of sentinel insect prey consumed (range of 0-1) across species from *Invertebrate-only exclosures* by A) treatment (Reduced Input vs. Biologically Based); B) distance from prairie strip, including 0 m (within strip), 1, 5, and 20 m into the adjacent row crop; and C) month (May- September) at the KBS-LTER MSCE in Hickory Corners, MI.

A)

Treatment	Sample Mean \pm SE
Reduced Input	0.54 \pm 0.01
Biologically Based	0.55 \pm 0.01
All	0.57 \pm 0.01

B)

	Sample Mean \pm SE			
Treatment	0 m	1 m	5 m	20 m
Reduced Input	0.69 \pm 0.02	0.61 \pm 0.02	0.54 \pm 0.02	0.46 \pm 0.02
Biologically Based	0.58 \pm 0.02	0.58 \pm 0.02	0.54 \pm 0.02	0.44 \pm 0.02
All	0.63 \pm 0.02	0.59 \pm 0.02	0.54 \pm 0.02	0.45 \pm 0.02

C)

	Sample Mean \pm SE				
Treatment	May	June	July	August	September
Reduced Input	0.53 \pm 0.02	0.68 \pm 0.02	0.59 \pm 0.03	0.43 \pm 0.03	0.62 \pm 0.02
Biologically Based	0.5 \pm 0.03	0.57 \pm 0.02	0.61 \pm 0.03	0.67 \pm 0.02	0.39 \pm 0.02
All	0.52 \pm 0.02	0.62 \pm 0.02	0.6 \pm 0.02	0.55 \pm 0.02	0.5 \pm 0.02

Table 4.2. Generalized Linear Model (GLM) negative binomial models were developed for 2022 for proportion consumed (range 0-1) of sentinel insect prey across species from *Invertebrate-only exclosures* based on known variables for treatment (Reduced Input vs. Biologically Based), month (May -September), and distance (0 m or within strip and 1, 5, and 20 m from strip edge), as well as the interactions between distance and treatment (D:T) or month and treatment (M:T). The models were ranked via their QAICc values and overall weight. The negative binomial model takes into consideration zero-inflation.

Best Model: Proportion Consumed \sim Treatment*Month + Distance							
Variable							
Treatment	Month	Distance	D:T	M:T	df	QAICc	Weight
+	+	+		+	14	566.2	0.460
+	+	+	+	+	17	567.2	0.278
+	+	+			10	568.4	0.155
+	+	+	+		3	569.2	0.106

Table 4.3. Mean and standard error (SE) for proportion of sentinel weed seeds consumed (range of 0-1) across species *from Invertebrate-only exclosures* by A) treatment (Reduced Input vs. Biologically Based); B) distance from prairie strip, including 0 m (within strip), 1, 5, and 20 m into the adjacent row crop; and C) month (May-September) at the KBS-LTER MSCE in Hickory Corners, MI.

A)

Treatment	Sample Mean \pm SE
Reduced Input	0.04 \pm 0.004
Biologically Based	0.04 \pm 0.004
All	0.04 \pm 0.003

B)

	Sample Mean \pm SE			
Treatment	0 m	1 m	5 m	20 m
Reduced Input	0.04 \pm 0.01	0.03 \pm 0.01	0.03 \pm 0.01	0.06 \pm 0.01
Biologically Based	0.04 \pm 0.01	0.04 \pm 0.01	0.03 \pm 0.01	0.04 \pm 0.01
All	0.04 \pm 0.01	0.04 \pm 0.01	0.03 \pm 0.01	0.05 \pm 0.01

C)

	Sample Mean \pm SE				
Treatment	May	June	July	August	September
Reduced Input	0.01 \pm 0.01	0.09 \pm 0.01	0.03 \pm 0.01	0.04 \pm 0.01	0.01 \pm 0.004
Biologically Based	0.001 \pm 0.001	0.09 \pm 0.01	0.03 \pm 0.01	0.05 \pm 0.01	0.01 \pm 0.003
All	0.01 \pm 0.003	0.09 \pm 0.01	0.03 \pm 0.004	0.04 \pm 0.01	0.01 \pm 0.003

Table 4.4. Prairie Strips perennial seed mixture, including 18 forbs and 4 warm-season grasses planted in April 2019. Kellogg Biological Station LTER Main Cropping Systems Experiment, Hickory Corners, MI.

Grass Species	Common Name	Seeds/ft²
<i>Andropogon gerardii</i>	Big Bluestem	0.92
<i>Bouteloua curtipendula</i>	Side-oats Grama	1.93
<i>Elymus canadensis</i>	Canada Wild Rye	0.48
<i>Schizachyrium scoparium</i>	Little Bluestem	3.44
	Total	6.77
Forb Species	Common Name	Seeds/ft²
<i>Achillea millefolium</i>	Yarrow	2.05
<i>Asclepias syriaca</i>	Common Milkweed	0.33
<i>Asclepias tuberosa</i>	Butterfly Milkweed	0.30
<i>Aster novae-angliae</i>	New England Aster	1.1.4
<i>Coreopsis lanceolata</i>	Lance-leaf Coreopsis	1.84
<i>Coreopsis tripteris</i>	Tall Coreopsis	0.26
<i>Desmodium canadense</i>	Showy Tick Trefoil	0.25
<i>Echinacea purpurea</i>	Purple Coneflower	0.61
<i>Lespedeza capitata</i>	Round-headed Bush Clover	0.30
<i>Monarda fistulosa</i>	Wild Bergamot	1.21
<i>Ratibida pinnata</i>	Yellow Coneflower	0.69
<i>Rudbeckia hirta</i>	Black-eyed Susan	5.28
<i>Silphium perfoliatum</i>	Cup Plant	0.04
<i>Solidago juncea</i>	Early Goldenrod	2.66
<i>Solidago nemoralis</i>	Old-field Goldenrod	2.75
<i>Tradescantia ohiensis</i>	Common Spiderwort	0.18
<i>Verbena stricta</i>	Hoary Vervain	0.96
<i>Zizia aurea</i>	Golden Alexander	0.72
	Total	21.57

Table 4.5. Details for agrochemical (fertilizer and pesticide) applications in 2018-2022 in the Reduced Input and Biologically Based treatments at the Kellogg Biological Station LTER Main Cropping Systems Experiment (MCSE), Hickory Corners, MI. See herbicide (<https://lter.kbs.msu.edu/datatables/160>), fertilizer (<https://lter.kbs.msu.edu/datatables/159>), and insecticide applications (<https://lter.kbs.msu.edu/datatables/161>) on the lter.kbs.msu.edu website.

Year	Treatment	Herbicide	Insecticide	Fertilizer
2018	Reduced Input	Herbicide Roundup Power Max (glyphosate 48.7%)	None	Fertilizer 0-0-60 potash fertilizer Ammonium sulfate (AMS)
2018	Biologically Based	None	None	
2019	Reduced Input	Herbicide PowerFlex HL Herbicide Roundup Power Max (glyphosate 48.7%)	NIS (Activator 90)	Fertilizer 28% UAN (28-0-0) Sulfur (0-0-0-85) Fertilizer 0-46-0 phosphate fertilizer Fertilizer 0-0-60 potash fertilizer Ammonium sulfate (AMS) Prairie Strip Custom Seed mix Fertilizer 28% UAN (28-0-0)
2019	Biologically Based	None	None	Prairie Strip Custom Seed mix
2020	Reduced Input	Dual II Magnum (s-metolachlor (+ safener)) Herbicide Roundup Power Max (glyphosate 48.7%)		Fertilizer 0-0-60 potash fertilizer Fertilizer 16.5-16.5-0-2.9 Ammonium sulfate (AMS)
2020	Biologically Based	None	None	None
2021	Reduced Input	Herbicide Roundup Power Max (glyphosate 48.7%)		Fertilizer 0-0-60 potash fertilizer Fertilizer 0-46-0 phosphate fertilizer Ammonium sulfate (AMS)
2021	Biologically Based	None	None	None
2022	Reduced Input	Herbicide PowerFlex HL		Fertilizer UAN 28% Fertilizer 0-46-0 phosphate fertilizer Fertilizer 0-0-60 potash fertilizer Sulfur (0-0-0-85)
2022	Biologically Based	None	None	None

Table 4.6. Mean and standard error (SE) for proportion sentinel insect prey consumed (range of 0-1) across species from *Open exclosures* by A) treatment (Reduced Input vs. Biologically Based); B) distance from prairie strip, including 0 m (within strip), 1, 5, and 20 m into the adjacent row crop; and C) month (May – September) at the KBS-LTER MSCE in Hickory Corners, MI.

A)

Treatment	Sample Mean \pm SE
Reduced Input	0.75 \pm 0.01
Biologically Based	0.69 \pm 0.01
All	0.72 \pm 0.01

B)

Distance (m)	Sample Mean \pm SE
0	0.8 \pm 0.01
1	0.74 \pm 0.02
5	0.69 \pm 0.02
20	0.66 \pm 0.02

CHAPTER FIVE: CONCLUSIONS AND FUTURE DIRECTIONS

As the human population increases, so too has the demand for food production, innovation, and expansion of agricultural practices. However, the simplification of diverse landscapes and use of intensified agriculture has resulted in global biodiversity loss. Agricultural landscapes need to be multifunctional, integrating ecosystem services to support both high-yields and ecosystem health. Establishing conservation techniques that enhance ecosystem services provided by arthropods, such as pollination, decomposition, or predation will benefit farmers and contribute to conservation efforts to improve biodiversity. Ground beetles or Carabids (Coleoptera: Carabidae) are beneficial predators commonly found in agricultural landscapes that provide insect pest and weed seed predation and serve as natural indicators of biodiversity. In this dissertation, I investigated the impact of long-term management practices in row crop agriculture on Carabid community structure, and the impact of prairie strips as a conservation intervention to enhance the biodiversity and ecosystem services provided by ground-dwelling arthropods. Here, I have addressed a valuable question raised by both researchers and the farming community on the spillover effects of prairie strip implementation in agriculture. Although carabids and beneficial predators represent one of many services provided by prairie strips, this dissertation contributes to growing research on conservation interventions to promote ecologically intensive agriculture that supports both ecosystem and human health.

Carabid Community Composition in Long-term Agriculture

In Chapter 1, I reviewed the impacts of intensified agricultural landscapes and field-level management on the biodiversity and ecosystem services of carabids. In agricultural systems, carabids are useful indicators of biodiversity and ecosystem health as they are globally abundant, well-studied, and active both above- and belowground. Carabids are impacted at local and landscape scales; landscape simplification that isolates semi-natural lands or non-crops areas within agriculture reduce the diversity of patch populations, and their associated potential as natural predators (Pulliam 1988; Hanski and Simberloff, 1997; Gardiner et al. 2010; Tscharrntke 2005; Landis 2017). Locally, carabid community diversity and predation potential are impacted by agronomic practices such as tillage or pesticide use. Tilling or plowing during either the spring before seeding the crop or in the fall after harvest directly disturb vulnerable adult or larval overwintering stages of carabids (Kirk 1973; Lindroth 1992; Lovei and Sunderland 1996;

Kladivko 2001; Muller et al. 2022). Furthermore, pesticide and herbicide applications limit carabid food resources such as weed seeds or insect prey both within the field and across broader agricultural landscapes (Holland and Luff 2000).

Time is a common limitation to biodiversity studies. Insect populations fluctuate with time depending on field or landscape conditions, and many studies on biodiversity decline or habitat response are short-term. The long-term effects of habitat fragmentation are understudied, and as shown by Haddad et al. (2015), habitat fragmentation and loss results in a time-delay for biodiversity decline as species adjust to new environmental conditions. In Chapter 2, I addressed this gap in knowledge on the long-term effects of agricultural management and the resulting carabid communities. After three decades of management on two conservation-oriented cropping treatments, I found that a) overall carabid activity-density (abundance) declined 58-76% and previously dominant species declined 94-98%; b) seed-eating carabids increased in activity-density in the organic treatment, likely as a result of weed density; and c) management changed prey availability and contributed to species turnover in the carabid community. Understanding carabid biology and response to changes in environmental conditions, especially long-term management, served as the foundation for my dissertation research in Chapters 3-4, the objectives of which were to investigate the impact of perennial prairie strips on carabid community composition and predation services.

Prairie Strips and Carabid Communities

Perennial semi-natural or non-crop habitat established in high-input agroecosystems have been proven to provide valuable habitat (Thomas et al. 2002; MacLeod et al. 2004) and contribute to increased diversity and abundance of carabids and ground-dwelling arthropod predators (Haan et al. 2021; Iuliano et al. 2024). As a novel conservation technique, prairie strips enhance ecosystem services and diversity of arthropod predators through strategic placement of perennial flowers and grasses in crop fields. An objective of this dissertation was to investigate the impact of prairie strip seeding (2019) through maturation (2022) on carabid community composition and provision of predation services at the KBS-LTER. Further, my dissertation research in Chapters 3-4 contribute to gaps in knowledge on the spillover effects of prairie strips into adjacent row crops, in particular, the potential for insect pest and weed seed predation valuable to Michigan farmers. In Chapter 2, I discussed how long-term management resulted in distinct carabid communities by cropping treatment; in Chapter 3 I further showed that treatment

is a significant factor in species response to prairie strip establishment. The organic cropping treatment (Biologically Based) supported higher diversity and twice the abundance of carabids than the conventional Reduced Input treatment one year after seeding, particularly for omnivorous or granivorous carabid species consuming prevalent weeds in the seedbank. I also found strong evidence that prairie strip establishment from 2019-2022 resulted in species turnover within both the prairie strip and field center, leading to more similar communities in both treatments by 2022 despite initial dissimilarity. I provide evidence that 11 carabid species initially found in the prairie strip in 2020 were found only at field center in 2022. This is critical, as it supports our initial hypothesis that perennial prairie strips established within crop fields contribute to increased biodiversity both within the strip, and into the crop. Further, as many of the species found only in the row crop were predators, these species may provide beneficial predation services on crop pests.

In Chapter 4 I investigated how prairie strip establishment at the KBS-LTER has contributed to insect pest and weed seed predation, and to what extent arthropod predation services extend into the row crop. It was important to study how system attributes (i.e. cropping treatment, distance from prairie strip, and time of season) also influence predation services. Using metal exclosures and sentinel insect predation cards, I contrasted the total predation by invertebrate arthropod predators to vertebrate predators (birds, rodents, etc.) in both the Reduced Input and Biologically Based treatments in 2022. Although sentinel prey exposed to both vertebrate and invertebrate predators resulted in ~70% total predation, invertebrate-only predation was on average > 50% in both treatments. Sentinel insect pest predation was highest within or near-to the prairie strip and decreased with distance into the row crop. Beneficial arthropod predators observed at the KBS-LTER include carabids (Carabidae), harvestmen (Opilionidae), spiders (Aranea), ants (Formicidae), and predatory wasps (Vespidae). Of these, spiders and harvestmen have been shown to respond positively to increases in semi-natural or non-crop habitat within arable fields, likely due to the availability of protective vegetation and alternative prey (Schmidt and Tscharntke 2005; Papura et al. 2020). Ants were the most common predator both within the field and prairie strip and likely contributed the most to predation. Helms et al. (2021) has shown that treatment significantly affects ant diversity and timing of predation services; in their study at the KBS-LTER, although ant activity was highest in the Reduced Input treatment post-harvest, ants were more consistent and effective predators

throughout the growing season within the Biologically Based treatment.

My dissertation research on predation services provided by arthropods also found a distinct correlation between service provision and time of growing season. As described in Chapters 1-3, seasonal emergence is an important factor affecting carabid diversity and abundance at the KBS-LTER. Carabid communities that emerge early spring vary in species richness and diversity from mid-season species and are critical for early suppression of crop pest populations. My research on arthropod predation in Chapter 4 shows that predation rates in the prairie strips were higher than in the row crop throughout the growing season, including early or late season; this distinction hints at the value of prairie strip habitat in providing a) protection from disturbance and b) alternative prey resources to support early or late-season predator communities present within the cropping treatments.

Overall Conclusions

In this dissertation, I have described the value of carabids as bioindicators within agroecosystems, given they are active above- and belowground and respond to local and landscape scale changes in land use. This dissertation provides evidence that communities of carabids are filtered by long-term agricultural management, in particular the reduction of available prey through pesticide application and management. Furthermore, establishing perennial prairie strip habitat directly within row crop agriculture increases the diversity and abundance of carabids within adjacent row crops. Although my research has demonstrated that prairie strips result in increased predation rates within and near-to strips by arthropod predators, in-field predation services remain variable. However, prairie strips are valuable refuge habitat for arthropod predators in high-input agroecosystems, particularly during early- and late-season when few alternative resources are available.

Insects are declining at alarming rates across the world. Current estimates place insect biodiversity decline at 45% (Wagner et al. 2020). Recently, Edwards et al. (2025) found that butterfly abundance declined by 1.3% annually from 2000-2020, or 22% after 20 years. Using citizen science data on butterfly observations, their analysis shows that butterfly species richness declined 28% in every continental US region studied, with the highest rates of decline in the Southwest, where warming temperatures threaten southern ranges of many species. Edwards et al. (2025) and others have suggested the causes for the decline in insect biodiversity are attributed to habitat loss, climate change, and pollution or agricultural pesticide use.

Agricultural advancement as a result of innovation in equipment, technology, or chemical use has reduced global famine. However, as insects are critical to the provision of services in agriculture, including the suppression of crop pests, pollination, and nutrient cycling, current rates of decline may threaten global food security. Climate change further exasperates the race to make agriculture more resilient and prevent biodiversity decline, as warming temperatures may shift the distribution or range of many pests or invasive species. Commodity crops such as rice, wheat, and corn are expected to decline in yield by 10-25% per degree of warming as a result of the impact of climate change on beneficial or pest species (Steffan-Dwenter et al. 2024). Thus, investing in conservation practices that contribute to resilient ecosystems is necessary for sustainable agriculture.

Interventions to restore biodiversity and ecosystem services can be guided by relevant agroecological theory and practice. Landscape heterogeneity, both compositional and configurational, contributes to biodiversity and supports ecosystem functioning (Tscharntke et al. 2005, 2007; Fahrig 2013). However, the continued intensification and expansion of agriculture poses a risk to maintaining the functional value of agroecosystems. Modern agricultural landscapes are dominated by monocultural row crops with little habitat diversity, both for efficiency in crop management and profitability. Habitat isolation and fragmentation contribute to biodiversity decline (Haddad et al. 2015) and disproportionately benefit generalist species over specialists (Pfeiffer et al. 2017).

Michigan's agriculture differs from other Midwest, US states in that it supports a diverse industry of fruits, vegetables, and grains among a landscape of forests, wetlands, grasslands, and urban developments. Here, the industry includes both smallholder farms practicing crop diversity to large monocultures of high-commodity crops, and a spectrum of organic to conventional agricultural practices. As such, conservation practices that support biodiversity or ecosystem services require strategic placement and flexibility. The 'intermediate landscape-complexity hypothesis' described by Tscharntke et al. (2005) distinguishes habitats with 2-20% semi-natural or non-crop habitat within the landscape as benefiting the most from conservation interventions. Identifying interested farmers and landowners within applicable intermediate-landscapes to establish prairie strips in Michigan is one of many strategies to increase biodiversity of natural predators and to support more diverse landscapes overall. Research conducted by Michigan State University scientists have used remote sensing technology to identify low-yielding areas of

arable lands (Basso et al. 2019). Across 10 Midwest, US states, ~26% of sampled corn fields (7.8 million ha) were low-yielding and could benefit from conservation interventions.

Conservation interventions such as perennial prairie strips provide necessary non-crop habitat to support biodiversity and service provision through protection from disturbance, alternative prey or floral resources, and overwintering habitat. MSU extension MiSTRIPS have created partial budgets to assist aspirational farmers with prairie strip implementation that suggest long-term profits from converting crops producing at <50% yield (Drobnak et al. 2024).

Engaging with farmers to meet their needs for pest management can be difficult given social and economic constraints (Prokopy et al. 2012). However, despite the literature on the benefits of prairie strips and federal support for prairie strip establishment under the Conservation Reserve Program (CRP), adoption remains low in Michigan. Future research on prairie strips and their establishment must collaborate with local farmers to better meet their needs for soil health, pollination or pest control, and economic support, and must encourage the active participation of the farming community.

It is necessary for future prairie strip research to investigate the impact on beneficial arthropod predators at both local and landscape scales to provide efficient conservation biological control. Scope is the primary limitation of this study; experiments at the KBS-LTER provide valuable information for initial application of novel conservation techniques or the ecological response of agricultural practices. However, every farm is different, whether by size, crop diversity, management, or the surrounding agricultural landscape. To best understand how prairie strips influence the biodiversity of beneficial arthropods and provision of pest predation services, future research must partner with Michigan farmers and growers to conduct on-farm trials. Feedback from such studies will improve our understanding of prairie strips as a conservation practice, and best practices for broader application and adoption of this conservation intervention.

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APPENDIX 1. FARMER ENGAGEMENT: BARRIERS AND OPPORTUNITIES FOR PRAIRIE STRIP ADOPTION

Michigan's diverse agricultural landscape will benefit from regenerative agricultural practices focused on crop resiliency and ecosystem health. In addition to the consequences of climatic effects, intensive agricultural practices in the Midwest have led to fragmented landscapes, biodiversity loss, and reduced soil and water quality. This continued growth is unsustainable and will require shifting from a culture of intensively managed crops to agroecosystems that support crop yield through integration of ecosystem services and regenerative practices (Bommarco et al. 2013). A potential solution that incorporates resilient agricultural practices with ecosystem benefits are prairie strips, or strategic plantings of native prairie vegetation directly into agricultural landscapes. Prairie strips provide valuable benefits to above and belowground biodiversity at local and landscape scales. By introducing native prairie vegetation within or surrounding crop fields, growers benefit from local biological control of insect and weed pests. Strips provide protection from agricultural disturbance and supplemental resources, and, as pollination is a key service to fruit and vegetable growers in Michigan, prairie strips also provide valuable pollinator nesting and nectar source (Kemmerling et al. 2023).

Row crop agriculture makes up 38% of agricultural land use in the Midwest, conventionally managed for corn, wheat, and soybean (Crossley et al. 2021). Basso et al. (2019) found that 7.8 million hectares of planted rowcrops in 10 Midwest states are low-yielding, and could be profitably converted to non-crop habitat, such as prairie strips. Not only will replacing prairie strips in zones of low productivity reduce labor, time, and money on behalf of the grower, but also improve the availability of quality habitat and resources for ecosystem health and biodiversity. Given the uncertainty of crop response to climate change, farmers may also benefit from regenerative agricultural practices that promote crop resiliency to drought, temperature extremes, or increased pest presence through provision of ecosystem services.

Michigan State University is invested in Michigan agriculture and has cultivated networks of farmers and extension programs. Over the last three years, the MSU-Extension MiSTRIPS program has advocated for prairie strip research and implementation in Michigan by hosting farmer education and demonstration days. As of 2019, Farmers can qualify for federal

payments to fund prairie strip establishment through the Farm Bill, including the Conservation Reserve Program (CRP-43) or Environmental Quality Incentives Program (EQUIP). However, adoption among rural farmers in Michigan remains low. Due to the diversity of the landscape and variety of fruit, vegetable, and grain crops in Michigan, growers here require greater flexibility and support when implementing conservation practices such as prairie strips. An annual survey conducted by KBS-LTER since 2017 found that 38% of Michigan farmers “had not heard of prairie strips”, while 2% had “significant knowledge of their use” (Guo et al. 2023). Further, a 2022 farmer panel survey by Marquart-Pyatt (2024) found that 22% of 300 surveyed Michigan farmers are “moderately interested” in continuing to use or using prairie strips in the future. This suggests a need to understand the barriers Michigan farmers face when establishing and maintaining prairie strips.

Interdisciplinary research within agroecosystems is necessary to fully understand ecological processes within and above the soil surface, and at local to landscape scales; however, I argue that community engaged research is also a vital component of this work. Agriculture exists in a “common-pool system” of resources including water and soil quality, nutrient availability, and ecosystem services (Eaton et al. 2022), suggesting the need for widespread implementation of regenerative practices. The literature on farmer perspectives of conservation practices presents a spectrum of factors that either motivate or deter farmers, including economic factors, social norms, and farm management. By shifting the focus from using farms as tools for conservation to encouraging farmer participation in the research and design of conservation practices, farmers may feel internally motivated towards environmental stewardship and sustainable practices. Isolating the barriers to adoption of prairie strips in Michigan will require community- engaged efforts with rural farmers, combined with MSU resources and extension networks.

APPROACH AND METHODS

I conducted a community engaged research project with conservation districts in Livingston, Barry, and Ionia, Michigan counties and hosted focus groups with rural farmers not currently in the MiSTRIPS program. The literature suggests a mixed-methods approach using both quantitative and qualitative data to address factors related to farmer perspectives (Prokopy et al. 2019). By working with conservation districts, I was able to filter a small sample of farmers per district with conservation-oriented mindsets or current practices (i.e. no- or reduced-tillage,

cover cropping). Furthermore, by working in districts independently, I was able to encourage a “place-based” approach to qualitative data collection, ensuring trust and familiarity within groups to help facilitate discussion (Prokopy et al. 2019). This further allowed me to compare the focus groups among counties (i.e. “sites”) to generate quantitative data.

Prior to conducting the focus groups, I introduced myself to the Conservation District boards in Ionia and Barry counties in the fall of 2024; I attended several Livingston County Conservation District meetings and a District 3 Farm Bureau meeting in 2023-2024 to propose the project and gain initial feedback. Working with representatives from each county, we met several times throughout the fall to prepare focus group details and determine the priorities for each district. Focus groups took place throughout February and March 2025.

Farmers included in these discussions came from diverse backgrounds, including landowners or renters, all crop or livestock types, new and generational farmers, and all ages or genders. This mix of perspectives allowed for discussion on the flexibility needed for prairie strip integration and management. Each focus group was approximately 2 hours, taking place from 9-11am at a local facility; Livingston County was conducted at the Livingston ESA, Barry County at the Pierce Cedar Creek Institute, and Ionia County at the MSU Clarksville Research Station. All participants were provided with refreshments throughout the event and reimbursed for attending (\$100/person). Focus groups were primarily discussion-based. Folders with printed agendas, resources and information were handed out to each participant. Pre- and post-surveys were used to evaluate participant knowledge of prairie strips and will remain anonymous with only necessary information for later analysis (age, type of farm, rental land or owned, new or generational farmer, etc.). Participants started with a pre-survey that addressed their knowledge of a) prairie strips as a regenerative agriculture resource, b) financial costs and USDA assistance, and c) benefits and disadvantages of prairie strips or plantings. This was followed by a short description of prairie strips, including a breakdown of implementation costs and how CRP-43 is designed to assist landowners with prairie strips installation and maintenance. After the presentations, we had brief breakout groups to facilitate discussion on topics related to a) both the advantages and disadvantages of prairie strips; b) based on the presentations, what are the barriers or bridges to adoption on your farm; and c) questions or concerns about prairie strips that were not addressed in the presentations. Using the “sticky note” method, we asked participants to record their responses to the discussion topics on sticky notes and place them on corresponding

paper sheets related to each topic. These will be used to record participant responses for later qualitative analysis. After the discussion session, participants were asked to complete a post-survey with the same questions as before, to record how their answers may have changed after both the information and discussion session, with an option for further comment.

OUTPUTS

I will work with members of the Ionia, Barry, and Livingston Conservation Districts and Farm Bureau to share my findings from this community-engaged research project at community meetings or Farmer Education Days. Results or pictures from the event will be shared with permission on associated websites or social media posts to encourage greater adoption of prairie strips on Michigan farms and share resources with a variety of Michigan farmers. I plan to produce a short (5-10 page) report on the results of the qualitative analysis and description of the focus groups to be given to each of the Conservation Districts and distributed at their discretion. Furthermore, I will present this data at local, regional, and national conferences attended by farmers, industry professionals, and academics.

I was invited to present on prairie strips and implementation at the Farmer Education Day hosted by the Livingston Conservation District and District 3 Farm Bureau in February 2025. Over 50 local farmers attended this meeting. I plan to further present the results of this data at the Great Lakes Fruit, Vegetable, and Farm Market Expo (GLEXPO) in 2025-26.

The data collected from these discussions will be published according to the interests of the Conservation Districts, Farm Bureau, and participating farmers. This will include publication in open-access journals of the qualitative analysis and methods, such as *Environmental Entomologist*, or the *Journal of Community Engagement and Scholarship*. I will also produce a short report to be published as an MSU-extension resource and provided to each of the Conservation Districts for use or distribution.

CONCLUSION

The long term, sustainable outcomes of this project will include the change in Michigan's agricultural landscape to include both more conservation-oriented farmers and diversity in farming practices. By engaging with farmers directly to identify opportunities and addressing place-based barriers to adoption of prairie strips, this project will lead to an increase in the number of Michigan farms and acreage enrolled in the Conservation Reserve Program (CRP) of the US Farm Bill, in particular CRP-43 which provides monetary incentives for farmers

converting previously arable land to prairie strips. Presenting my research at Conservation District and Farm Bureau meetings, as well as demonstration days held by partnering organizations will facilitate trust and partnerships between MSU researchers, MSU-extension, Conservation Districts, and participating farmers. Lastly, to adapt for an inconsistent climatic and economic future, this project will facilitate the adoption of a “resilient mindset” through place-based, regenerative agricultural management on Michigan farms.

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Table 5.1. Summary table of outcomes, outputs, activities, inputs, and evaluation

Expected Outcomes	Inputs and Activities	Outputs	Evaluation/Monitoring Plan; Measurement Methods
<p>Learning Outcomes:</p> <ul style="list-style-type: none"> • Develop a better understanding of the motivations or barriers to adoption of conservation prairie plantings on Michigan farms • Improve access to knowledge and resources on native prairie plantings as a conservation practice on Michigan farms • Increase the scope of MSU-extension MiSTRIPS program to include more diverse farmers in Barry, Ionia, and Livingston townships <p>Action Outcomes:</p> <ul style="list-style-type: none"> • Increase the number of farms and acreage in Michigan utilizing native prairie plantings as a conservation practice • Facilitate the adoption of a “resilient mindset” through place-based, regenerative agricultural management on Michigan farms 	<p>Materials: Printed information and resource pamphlets and necessary materials for focus groups</p> <p>Resources: Collaboration and network of outreach and education Knowledge and experience working with prairie strips</p> <p>Effort: Project coordination, driving to meet with farmers and project partners; Regular meetings with Conservation District and Farm Bureau partners</p>	<p>Qualitative data analysis of farmer perspectives on barriers to prairie strip adoption from focus group discussions</p> <p>Quantitative comparison of county results</p> <p>Production of presentations for Conservation District and Farm Bureau meetings, Farmer Education Day</p> <p>Extension publications (brief report)</p> <p>Open-access peer-reviewed publication in academic journal</p>	<p>Evaluation of activity, focus group analysis (qualitative) and discussion answers with Conservation Districts and MI Farm Bureau partners</p> <p>Pre/Post survey from focus groups on participant knowledge of prairie strips and implementation</p> <p>Number of published articles, extension or outreach materials Number of presentations or extension talks</p> <p>Number of farmers interviewed, number of farmers at focus groups, and number of farmers at demonstration or education days</p>

FOCUS GROUP AGENDA

Agenda (8:30 – 11am)

- **30 mins (8:30-9am) – Filter in and Introduction (Sign-in on worksheet)**
 - o *Welcome, thank you for attending! Today we are going to discuss the barriers and opportunities for adoption of prairie strips. Before we start, please help yourself to coffee, tea, and some snacks. Please sign in at the front.*
- **10 mins (9-9:10am) – Consent form and Pre-Survey**
 - o *Before we begin our discussions today, I first need everyone to please read and sign the consent form on the right-hand side of your folder. This is an anonymous survey and focus group, your personal information will not be released or alluded to in any published resources or data. I do need your signature on the sign-in sheet to indicate you received your gift card after today's discussion.*
 - o *After the consent form, I will now ask you to please fill out the pre-survey on the right-side of the folder. We will also take a post-survey after our discussions today. I'll give you ~ 5 mins to complete this, feel free to use bullet points.*
- **10 mins (9:10-9:20) – Prairie Strip Introduction**
 - o *Before we start are there any questions?*
 - o *Prairie Strips are the strategic planting of perennial prairie flowers and grasses within crop fields. Much of the Midwest was previously in prairie or grasslands before settlement, and native prairie plants provide beneficial ecosystem services, including season-long flowering and refuge habitat. They also sequester carbon, and reduce the flow of soil, water, and nutrients from entering local water resources and contributing to non-point source pollution.*
 - o *In 2019, prairie strips were included under the Conservation Reserve Program (CRP) as CP-43 in the US Farm Bill.*
- **40 mins (9:20-10am) – Small Group Discussions**
 - o *Please break out into small groups of 3-5 people. Use the “Focus Group Questions” as a guide to lead your discussion. I will float around the room and join in conversations or answer questions the best I can. Use the sticky notes to write down individual thoughts or points and place them on the large flipchart.*
- **10 mins (10-10:15am) – Break**
 - o *quick break to eat, drink or use the bathroom*
- **30 mins (10:15-10:45am) Large-group Discussion**
 - o *As a large group, discuss the key points from small-group flipcharts. Facilitator (Cindy) write down the key notes from this large-group discussion for later analysis.*
- **15 mins (10:45-11am) Wrap-up and Questions**
 - o *Answer last minute questions; clean-up all supplies*

FOCUS GROUP PRE-SURVEYS

Name:

Age:

Gender:

1. Briefly describe your farming operation (dairy, beef, pasture, vegetable, row crop, orchard, poultry, etc.). Do you own or rent the land you operate on?
2. How would you describe regenerative or sustainable agriculture?
3. Have you conducted regenerative or sustainable agricultural management on your farm? If no, why not?
4. Have you heard of perennial prairie strips or prairie plantings? If yes, have you or would you install this practice on your farm?
5. Have you previously worked with the Conservation District? If yes, in what way? If not, can you briefly explain why you have not?
6. What do you see are the key issues for agriculture in the future? What questions would you like to see addressed by agricultural researchers or extension personnel?

Thank you for participating in this survey!

FOCUS GROUP POST-SURVEYS

Name:

1. How would you describe regenerative or sustainable agriculture?
2. Have you or would you conduct regenerative or sustainable agricultural management on your farm? Why or why not?
3. How would you describe perennial prairie strips or prairie plantings? After participating in this workshop, would you be interested in establishing prairie plantings on your farm? Why or why not?
4. After participating in this workshop, would you be interested in working with the Conservation District in the future? Why or why not?
5. What do you see are the key issues for agriculture in the future? What questions would you like to see addressed by agricultural researchers or extension personnel?

Thank you for participating in this survey!

FOCUS GROUP QUESTIONS

1. What do you see are the advantages and disadvantages of prairie plantings (in general)?

2. Based on today's discussion, what do you think are the barriers or bridges to adoption of prairie plantings on your farm specifically?

3. What questions, concerns, or comments about prairie plantings do you have that were not addressed in today's presentations?

4. What do you see as the best way to access or share information about regenerative or sustainable agriculture?