HABITAT MANAGEMENT AND LANDSCAPE INFLUENCE *CRIOCERIS ASPARAGI* (COLEOPTERA: CHRYSOMELIDAE) OVERWINTERING BIOLOGY AND POPULATION DYNAMICS

By

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ABSTRACT

HABITAT MANAGEMENT AND LANDSCAPE INFLUENCE *CRIOCERIS ASPARAGI* (COLEOPTERA: CHRYSOMELIDAE) OVERWINTERING BIOLOGY AND POPULATION DYNAMICS

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Pest management of agricultural insect pests has often been focused on utilizing chemical control methods. However, managing habitats within and surrounding the crop field at varying spatial scales can be an effective and more sustainable means of controlling insect pest populations. In this thesis, I investigated the impacts of the surrounding habitat and landscapes on the overwintering biology and population dynamics of the common asparagus beetle (*Crioceris asparagi* L.) in commercial asparagus agroecosystems. During the winter of 2019-2020, I found that a majority of asparagus beetles were overwintering within asparagus fields, with beetle abundance being 23 times higher than field margins and 8 times higher than surrounding woodlots. In field experiments, asparagus beetle overwintering survival was highest when using deciduous leaves as overwintering habitat. At a landscape scale, the effect of the surrounding landscape varied between Oceana and Cass counties. When counties were combined, the proportion of semi-natural habitat (deciduous forest, evergreen forest, grassland) surrounding commercial asparagus fields was positively related to asparagus beetle abundance in asparagus fields. These results demonstrated that semi-natural habitats can potentially provide resources to not only beneficial insects, as previously thought, but pest populations as well. Both edge density and Shannon's Diversity Index (SHDI) were positively related at lower spatial scales and negatively related at higher spatial scales to the abundance of asparagus beetles in asparagus fields. Ultimately, my results suggest that both local and landscape level factors are influencing the overwintering biology and population dynamics of the common asparagus beetle.

I dedicate this thesis to my partner, Jason, and my family for their unlimited love and support.

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CHAPTER 1:

Habitat and landscape management of *Crioceris asparagi* in asparagus agroecosystems

Introduction

Popular for human consumption and its medicinal properties, asparagus (*Asparagus officinalis* L.) has been highly valued since its domestication by the Greeks and Romans traced back to as early as 65 A.D (Luzny, 1979). Originating in Eastern Europe, Caucasus, and Siberia (Sturtevant, 1890), asparagus is now cultivated throughout North America, South America, Europe, Asia, Africa, and Australia. Asparagus was originally brought to North America by early colonists from Europe and was thriving in New England by 1672 (LeSage et al. 2008). There are over 150 species in the *Asparagus* genus that are herbaceous perennials, woody shrubs, and vines (Ellison and Kinelski, 1986, Clifford and Conran, 1987), yet *A. officinalis* is the only species cultivated for human consumption. Asparagus is a good source of folic acid, vitamin C, thiamin, vitamin B6, potassium, and other micronutrients (Borris and Brunke 2006). Being unique as one of the few perennial vegetable crops available early in the spring, the cultivation of asparagus has grown exponentially throughout the globe in recent years.

Currently, asparagus is grown in 44 countries, with China, Peru, and Mexico as the leaders in tonnes of asparagus produced (FAOSTAT 2017). In the United States, 8,780 hectares of asparagus was harvested in 2018 yielding 35,460 tonnes (FAOSTAT 2018). With Michigan, California, and Washington as the lead producing states, the value of asparagus production nationally is approximately $70 million annually (AgMRC 2017). In 2019, Michigan producers sold over 10 million kg of asparagus, and ranked first in total asparagus acreage, with growers harvesting approximately 9,500 acres annually (MDARD 2019). Asparagus is considered a high-value crop, with an estimated value of more than $23 million annually in Michigan (MDARD

2019). The western region of Michigan's lower peninsula has the ideal climate and soil composition to be the country's leading asparagus producer, with a mature asparagus field picked approximately 45 times a season (personal communications, Ben Werling).

Asparagus is a versatile crop, as it can be consumed fresh, canned, or frozen. In 2019, approximately 65% of Michigan's asparagus production was sold fresh and 35% was processed. Of the processed asparagus, 75% was frozen and 25% was canned (personal communications, John Bakker 2020). If managed attentively, an asparagus field can thrive for up to 20 years with an individual asparagus plant capable of producing over 25 marketable spears throughout the harvest period. Michigan is unique for its harvesting methods of asparagus, using the 'hand-snapping' method which yields more tender and flavorful spears in comparison to mechanical harvesting methods (MDARD 2019). After the harvest season, growers allow the fern, the photosynthetic part of the plant, to grow and create root storage metabolites for the following year's harvest. Herbivore pests, such as asparagus beetles continue to create damage after harvest resulting in a reduction in asparagus yield.

Asparagus Beetles

Life history- Originating in the Mediterranean region, the common asparagus beetle (*Crioceris asparagi* (L.), Coleoptera: Chrysomelidae) was initially introduced to the United States in New York around 1860 (Chittenden 1917). Asparagus beetles, adults and pupae, most likely entered the United States by the transportation of root crowns and soil (Chittenden 1917, Caesar 1938). Asparagus beetles are able to create substantial damage to the plant during and after the harvest season. Although current studies on the biology of this pest are limited, they have caused considerable economic damage to asparagus production in the Midwestern United States. First reported in Michigan in 1898 (Chittenden 1898), asparagus beetle damage now costs Michigan farmers over $1 million annually including load rejections of harvested spears, mowing down infested fields before harvest, sorting costs to remove infested spears, and chemical control measures (personal communications, John Bakker). Asparagus harvest begins soon after adult beetles emerge from their overwintering state with adults immediately mating and ovipositing on spears (Chittenden 1896). Female beetles use the epithelium of the pedicel to secrete an adhesive to attach eggs to the plant tissue (Gupta and Riley 1967). Once adhered, eggs are nearly impossible to remove, requiring a force of about 8,650 times the weight of an egg to remove (Voigt and Gorb 2010). Consequently, the inability to remove beetle eggs from harvestable spears significantly reduces the market value of the crop. Furthermore, using their chewing mandibles, beetles remove the plant's cladophylls and epidermis as larvae and adults (Chittenden 1917). After harvest, both larvae and adults feed on the cladophylls and axillary branches of the asparagus fern and spear, reducing the photosynthetic capability of the plant (Grafius and Hutchison 1995).

Asparagus beetles typically undergo two generations throughout the growing season but can sometimes complete three generations in temperate regions (Dingler 1934, Capinera and Lilly 1975, Taylor and Harcourt 1975). Gray and elongate-oval eggs are 1-2mm long and are placed in rows of 3-10 eggs on foliage, stems, and flower buds (Fig 1.1A, Voigt and Gorb 2010). After 3-8 days, larvae emerge and grow; they are dark to olive gray and are on average 8mm in length by their fourth instar (Fig. 1.1B). Depending on the temperature, larvae typically feed between 10-15 days and undergo four successive instars (Drake and Harris 1932). The larvae have three pairs of legs and five pairs of anal prolegs which allow them to grasp onto the plant when feeding (Capinera, 2001). As larvae feed on the plant, they excrete a black "molasses-like" fluid, consisting of fecal material, which discolors the plant tissue and creates further damage to the crop (Drake and Harris 1932). Once they reach pupation, they drop from the plant and dig into the soil to create a pupal cell consisting of oral secretions and soil. On average, the pupal stage lasts for 7-12 days (Drake and Harris 1932). After pupation, beetles develop into their final adult stage measuring ~6-7mm in length (Fig. 1.1C, Chittenden 1917). Once temperatures decrease and daylight shortens in the fall, beetles begin to enter winter diapause as adults. The stages of the asparagus beetle life cycle are depicted in Figure 1.2.

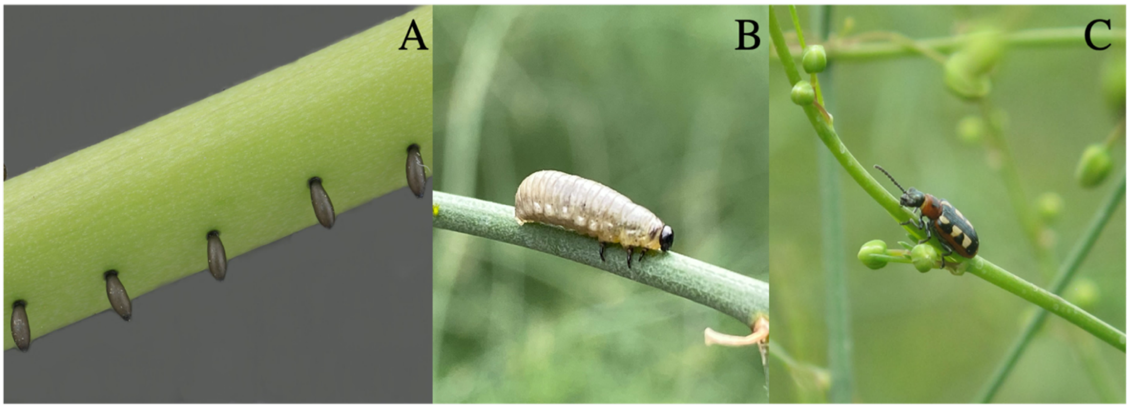

Figure 1.1 Asparagus beetles lay eggs on spears during harvest (A), which reduces spear quality. These eggs do not develop into larvae during harvest, as spears are picked before they can hatch. After harvest during the fern stage, larvae (B) hatch from eggs, defoliate the fern and develop into adult beetles (C). There are typically two or three generations of asparagus beetles in Michigan with the last generation of adults seeking out overwintering shelter to survive the winter. They emerge in the spring to feed, mate and lay eggs. Photos by Jennifer Zavalnitskaya and Zsofia Szendrei.

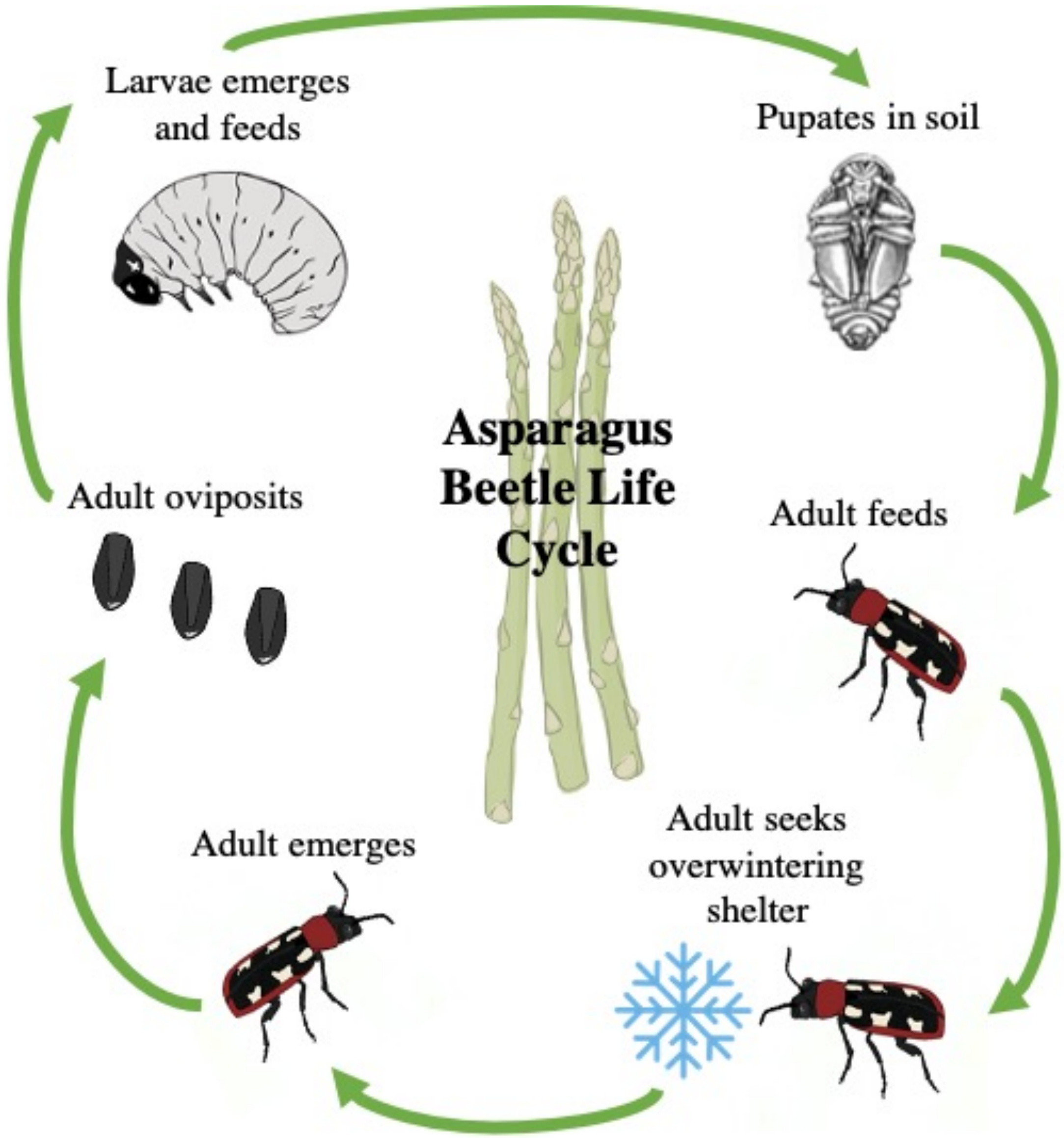

Figure 1.2 Asparagus beetle life cycle. Eggs, larvae, pupae, and adults. Illustrated by E. Darling and B. Demarco.

Current and future pest management strategies

Chemical control- Currently, the primary management strategy for asparagus beetles is the foliar application of broad-spectrum insecticides such as carbamates, organophosphates, and pyrethroids (Hutchison et al. 1990). These insecticides seem to initially eradicate adult beetles, but subsequent flushes of beetles appear soon after for reasons unknown. Economic thresholds have been developed as a useful tool for growers to keep beetle populations under control. Based on the examination of 100 plants per field for the presence of beetles or eggs, the threshold is met if >2% of spears observed contain eggs and if >5-10% are infested with adults (Delahaut 2005). Due to worker safety and pre-harvest interval requirements, growers find it difficult to control beetles effectively throughout harvest with broad-spectrum insecticides which typically require re-entry intervals of 12-72h (Bird et al. 2014). This can be problematic when harvesting the crop, thus safer options with shorter re-entry periods such as spinosad and spinetoram have been recommended but have only been labeled for post-harvest protection of ferns (Kuhar et al. 2006). To create a more efficient integrated pest management plan, other management strategies should be considered.

Biocontrol- Utilizing natural enemies to reduce pest pressure can help create a more sustainable and profitable integrated pest management (IPM) plan (Bale et al 2007, Naranjo et al. 2015). Although chemical control is the primary management strategy for asparagus beetles, biological control can also be used as part of an IPM strategy. There are several insect predators that feed on asparagus beetles in their natural environment, such as Coccinellidae and Staphylinidae (Ingrao et al. 2017). Natural enemies and predators are typically distributed along field borders and edges in asparagus agroecosystems (Ingrao et al. 2017). The primary parasitoid of asparagus beetle is *Tetrastichus coeruleus* (Nees) (Hymenoptera: Eulophidae) which is an egg-larval parasitoid that is native to Europe, but was first observed in northeastern United States in 1863 (Riley and Walsh 1869), and was later used as a biological control agent. In 1937, the parasitoid was sent from Ohio to Washington to help control asparagus beetles with great success, and since then has been observed in Michigan (Johansen 1957).

Cultural control- Various types of sanitation are used as physical and cultural control management within asparagus agroecosystems. Cultural control methods include leaving a small portion of the crop unharvested to attract congregations of beetles (Day and Kuhar 2017). Oftentimes, volunteer asparagus that emerges near fields is either chemically or mechanically removed to eliminate additional resources (Delahaut 2005). Historically, when summer temperatures peaked, the "brushing method" was used, which involved beating the fern so that larvae would drop to the ground to be exposed to excessive heat causing death (Chittenden 1917). Current physical control methods include removing remaining crop debris after harvest in the spring or fall that is used by beetles as overwintering habitat (Buchanan et al. 2015, John Bakker, personal communications).

Overwintering biology

Insect overwintering- Overwintering is a crucial yet often dangerous process that a majority of insects undergo in temperate climates. Throughout overwintering, insects are exposed to extreme physical conditions; thus, selection of an overwintering habitat can be imperative to survival. Although most insects undergo some form of hibernation, they have acquired varying physiological, behavioral, and biochemical adaptations to the harsh environment (Danks 1987). Some insects go into complete hibernation, while others remain somewhat active. When diapause is triggered by the environment, it is considered 'facultative' diapause. Conversely, when diapause occurs in each generation, regardless of environmental cues, it is considered 'obligatory' diapause (Denlinger 2009). Insect populations that enter a full diapause throughout the winter have the advantage of a higher cold tolerance and a decreased danger of starvation (Mansingh 1971). Due to the lack of mobility, the overwintering process can also include increased exposure to unfavorable overwintering site conditions, such as desiccation, drowning or increased predation rates (Leather et al. 1993).

Asparagus beetle overwintering- Overwintering biology of asparagus beetles is poorly understood and has not been well documented. Asparagus beetles have been observed overwintering both within and surrounding asparagus fields. Specifically, they have been found overwintering in various substrates such as decaying plant material, woody debris, loose bark, and hollow asparagus stalks (Chittenden 1917, Drake and Harris 1932). Substrates like deciduous leaves and sometimes tree bark are often found both in and surrounding asparagus fields. However, an understanding of how the composition of these habitats and overwintering substrates affect asparagus beetle overwintering success remains unknown. Surrounding non-crop habitats can provide overwintering sites for both natural enemy and pest populations within agroecosystems (Tscharntke et al. 2016, Landis et al. 2000). Although little is known about the impact of ground cover and adjacent vegetation on pests, non-crop habitat can be a source for pest populations throughout multiple studies (Blitzer et al. 2012, Power and Mitchell 2004, Tscharntke et al. 2016). Consequently, investigating the composition of ground cover and adjacent vegetation throughout asparagus fields and surrounding non-crop habitat could be useful in understanding more about asparagus beetle overwintering and population dynamics.

I assessed asparagus beetle overwintering success in various habitats and substrates within asparagus agroecosystems in western Michigan. Understanding the overwintering biology of an insect pest can be useful in creating more efficient pest management strategies. By being able to estimate overwintering mortality and surveying insect populations prior to overwintering, the abundance of pests in the following season can be predicted (Leather et. al 1993). For example, overwintering pine beauty moth, *Panolis flammea,* pupal abundances can be used to predict the need to implement control measures (Stoakley 1977).

Habitat and Landscape Management

Habitat management- Pest populations may be impacted at local or regional spatial scales by both surrounding crop and non-crop habitats (Landis and Marino 1999). On a local scale, asparagus beetles and other asparagus pests tend to be distributed primarily along field edges, rather than the interior of the field (Morrison and Szendrei 2013, Ingrao et al. 2017). Consequently, asparagus miners (*Ophiomyia simplex,* Diptera: Agromyzidae) are distributed evenly throughout the field during their first generation, but then become primarily distributed near field edges during their second generation (Morrison and Szendrei 2013). This change in spatial distribution could be due to the presence of additional food sources or overwintering sites in the surrounding habitat. Semi-natural habitats, such as woodlots or floral strips, provide habitat to insect pests throughout the winter, resulting in a pest source in the spring (Leather et al. 1993, Geiger et al. 2005, Bianchi et al. 2006). However, previous studies have found that these surrounding semi-natural habitats are also able to provide additional habitat and resources to natural enemies and predators, resulting in lower pest populations in crop fields (Landis et al. 2000, Blaauw and Isaacs 2015, Bianchi et al. 2006). Although semi-natural habitat can sometimes suppress pest populations, that is not always the case (Tscharntke et al. 2016). For instance, the addition of surrounding floral strips had no impact on the biological control of asparagus miners within crop fields (Buchanan et al. 2018).

Landscape management- When managing agricultural pest populations, pest management efforts are typically targeted within the field, but surrounding natural and cropped landscapes can play a role in pest population dynamics as well. There are two essential components needed to describe a landscape; the landscape composition which is the area covered by a land cover type, and the landscape configuration which is the spatial arrangement of land covers within the landscape (Dunning et al. 1992). In some insect pests, such as pollen beetles, pest abundance is positively related to the proportion of surrounding woody areas, which could be a result of the pest's overwintering site preference (Zaller et al. 2008). In other systems, pest abundance is negatively related to the proportion of nearby woody areas. This could be due to the increased presence of natural enemies due to increased habitat availability (Ingrao et al. 2017, Landis et al. 2000). Thus, other landscape characteristics that could be impacting asparagus herbivore abundance must be considered. Although asparagus beetles are not considered strong fliers, they have been observed overwintering in surrounding landscapes, oftentimes woodlots. Past studies have demonstrated that the landscape configuration surrounding crop fields can influence arthropod populations as well (Haan et al. 2020, Gallé et al 2018). For instance, in rice agroecosystems the diversity of land cover has a negative impact on herbivore populations (Dominik et al. 2018). Other effects of landscape configuration such as edge density, connectivity, and field size can impact pest populations (Mitchell et al. 2014, Zhang et al. 2020). It is crucial to assess how different landscape compositions and configurations impact asparagus beetle survival and overall population dynamics throughout asparagus agroecosystems. By better understanding how factors in surrounding landscapes, locally and regionally, impact pest populations within crop fields, more targeted pest management strategies can be developed.

Thesis objectives

The goal of this thesis was to develop more effective control measures for asparagus beetles in Michigan asparagus production by investigating their overwintering biology and population dynamics at both local and landscape scales.

Objective I: Investigate the influence of local within field habitat and adjacent semi-natural habitat characteristics on asparagus beetle population dynamics

Sub-objectives:

A. Determine which habitat and substrate types throughout asparagus agroecosystems affect asparagus beetle overwintering beetle survival and mortality.

B. Identify characteristics of trees (i.e., species, DBH, bark rating) along the edges of asparagus fields in the surrounding semi-natural habitats that affect overwintering beetle abundance.

Objective II: Investigate the influence of surrounding landscapes on asparagus beetle population dynamics.

Sub-objectives:

A. Identify effects of the surrounding landscape composition and configuration on the abundance of asparagus beetles within asparagus agroecosystems.

B. Determine how landscape factors influence asparagus beetle abundance at varying spatial scales.

The findings of this thesis will be used to develop more efficient and sustainable habitat management strategies to reduce asparagus beetle populations within commercial asparagus agroecosystems. Specifically, the results of chapter two will suggest where throughout the asparagus agroecosystem growers should focus management efforts and which types of crop residue and substrates should be managed. Furthermore, the third chapter will expand current knowledge on how the composition and configuration of the greater landscape can affect asparagus beetle populations and help predict which types of landscapes may have higher beetle abundances. Ultimately, these results will demonstrate the importance of considering habitat management and the surrounding landscape on agricultural pest populations.

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CHAPTER 2:

Overwintering of *Crioceris asparagi* is mediated by asparagus field and adjacent semi-natural habitat

Introduction

Agroecosystems are often composed of a patchwork of crop and natural habitats that provide resources to a variety of arthropods (Bianchi 2006, Tscharntke et al. 2012). Non-crop habitats around crop fields, such as woodlots, windbreaks, hedge rows, and weedy field margins have been promoted to enhance natural enemy populations as a form of pest management (Woltz et al. 2012, Blaauw and Isaacs 2015, Tschumi et al. 2015, Buchanan et al. 2018). However, these habitats can provide food and shelter for a variety of arthropods, not just beneficial taxa (Rusch et al. 2010, Tscharntke et al. 2016). The types of arthropod communities at the interface of crop and natural areas can be indicative of the ecological role non-crop habitats play for agriculture.

When surrounding semi-natural habitat becomes a source of pests in the crop, the mechanisms and the resulting negative effects must be evaluated and mitigated with sustainable pest management (Tscharntke et al. 2016, Dunning et al. 1992, Blitzer et al. 2012). As a first step, we should consider how major pest species use the non-crop habitat around crop fields. For example, the bird cherry-oat aphid (*Rhopalosiphum padi* Hemiptera: Aphididae) is a major pest of cereal crops; they utilize vegetation that is commonly found in non-crop habitats for overwintering habitat (Leather 1993). In fact, in crops that decline at the end of the growing season, provisioning of overwintering habitats for pests may be one of the most important roles semi-natural habitats play in pest population maintenance (Rusch et al. 2010, Leather 1993). Uncultivated habitats near crop fields may increase availability of overwintering sites for pests, for example tree bark is used by overwintering brown marmorated stink bugs (*Halyomorpha* *halys*; Hemiptera: Pentatomidae, Ueno and Shoji 1978, Sivakoff et al. 2013). By identifying environmental characteristics that promote pest overwintering survival, control measures could be implemented to reduce overwintering habitat suitability and focus monitoring and management where pest pressure is expected to be highest. For example, coffee berry borers (*Hypothenemus hampei*: Coleoptera: Curculionidae) overwinter in fallen berries after harvest thus, growers are recommended to remove these berries to manage overwintering populations (Avelino et al. 2012). In some natural habitats, specific plant species are essential for parasitoid overwintering success (Corbett and Rosenheim 1996), so it is crucial to investigate whether the same is true for pest species.

The focus of this study was the common asparagus beetle (*Crioceris asparagi* Coleoptera: Chrysomelidae), a specialist pest of asparagus across North America (Morrison and Szendrei 2014). Thus far, most of the research on this pest has focused on its biology during the growing season (Ingrao et al. 2017, Capinera and Lilly 1975, Chittenden 1917) while little is known about its overwintering behavior. To improve our understanding about asparagus beetle overwintering, I (1) assessed effects of habitat type on the abundance and survival of asparagus beetles, (2) investigated how different overwintering substrates influenced asparagus beetle survival, and (3) evaluated the impact of tree characteristics along adjacent semi-natural habitats on asparagus beetle abundance.

Materials and Methods

Summer and fall beetle surveys

To determine asparagus beetle population dynamics and locate high-density beetle aggregations, commercial asparagus fields were surveyed using transects established along the field edge in Oceana and Cass counties (Table S2.1). In 2019, seven fields were surveyed three times from August 7th to September 6th. In 2020, ten fields were surveyed two to three times from July 21st to September 25th. Transects (25m x 1m) were established along the edge of asparagus fields that were bordered by woodlots. Between each transect a buffer (50m x 1m) was created, with the exception of one smaller field (Fig 2.1). In each transect, I counted asparagus beetle eggs, larvae and adults found on the side of the fern facing the woods. Number of transects varied among fields based on the area of the asparagus field ranging from 5-10 transects per field.

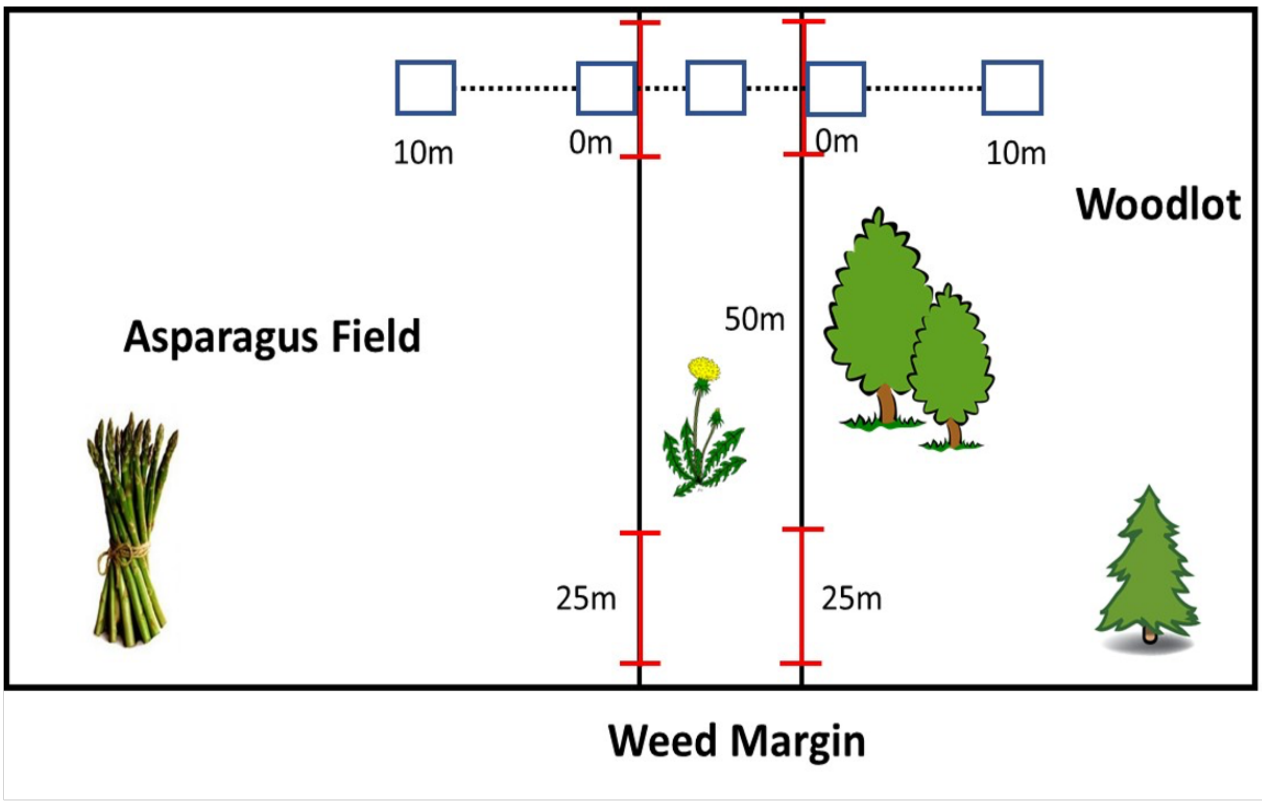

Figure 2.1 Habitat types that were sampled for overwintering asparagus beetles in commercial asparagus farms in Michigan. Red lines represent 25m asparagus transects visually surveyed for adult and larval stages in the summer and fall. Each 25m transect was spaced 50m apart and there were 5-10 transects per field. Black dotted lines represent 10m transects conducted perpendicular to the field edge into asparagus fields, weed margins, and woodlots. Blue boxes represent $1m^2$ quadrat samples along transects which were taken in late November 2019.

Overwintering beetle sampling

Overwintering asparagus beetles within and surrounding commercial asparagus fields were sampled in the winter of 2019-2020 by collecting substrate from the soil surface along transects in seven commercial asparagus fields throughout Oceana and Cass counties. Sampling was conducted along transects established in three habitat types: asparagus fields, weed margins, and surrounding woodlots. Transects (25m) were established in-between the asparagus fields and surrounding woodlots spaced 50m apart from each other. A starting point along the 25m beetle population transects was selected randomly. Three parallel transects (10m x 2m) were surveyed through each of the three habitat types (Fig. 2.1). Two $1m^2$ soil surface substrate samples were taken randomly from each transect. For each sample, a $1m^2$ quadrat was placed onto the ground and all contents above the ground were placed into a plastic bag and labelled. Samples were returned to the laboratory, stored at 4.5°C until samples could be processed by visually searching the contents for beetles. The particular substrate where each overwintering beetle was found in (e.g., leaves, soil, stalks) and if the beetle was alive or dead was noted.

Overwintering cage experimental design

Beginning in the fall of 2019, a field study was conducted at two locations, the Michigan Asparagus Research farm in Hart, MI located in Oceana county, and the Michigan State University Entomology research farm in East Lansing, MI located in Ingham county to evaluate overwintering survival in different substrates. Treatments for this experiment comprised of five different types of substrates commonly found in asparagus agroecosystems (Fig. 2.2), including hollow asparagus stalks (0.4kg/cage), needles from coniferous trees (0.6kg/cage), leaves from deciduous trees (0.2kg/cage), thin bark (0.6kg/cage, 0.1mm-5mm) and thick bark (1.1kg/cage, >5mm). Hollow asparagus stalks were collected at a commercial asparagus field (Hart, MI).

Decomposing coniferous foliage, dominantly *Pinus strobus* and *Picea pungens* needles, was collected off the ground in a woodlot surrounding a commercial asparagus field (Hart, MI). Decomposing deciduous leaves, thin bark, and thick bark were collected off the ground from the Baker Woodlot and Rajendra Neotropical Migrant Bird Sanctuary (East Lansing, MI). Both bark types were collected off the ground surrounding nearby trees of various species: *Acer saccharum, Ulmus thomasii, Prunus serotina, Liriodendron tulipifera, Betula alleghaniensis, Fagus grandifolia, Acer saccharinum, Quercus rubra, Sassafras albidum, Quercus alba, Tilia americana* and *Quercus macrocarpa*.

Figure 2.2 Overwintering cages were used to conduct a common garden experiment to determine which overwintering substrates promoted asparagus beetle survival. This experiment took place in Hart and East Lansing, Michigan from 2019-2020. Treatments used for this experiment included five substrates commonly found throughout asparagus agroecosystems: thin bark, thick bar, coniferous leaves, hollow asparagus stalks, and deciduous leaves. Ten beetles were placed into each cage in the late fall and collected in the early spring of the following year.

Overwintering cages (0.5m x 0.5m x 0.1524m) were built using untreated pine wood (15.24cm x 2.54cm) serving as the frame, and landscape cloth (101.6cm x 1097.28cm, natural weed block, Vigoro©, Lake Forest, IL) was adhered to the bottom with a staple gun (Arrow© TacMate, Los Angeles, CA). Aluminum window screening (60.96cm x 30.48cm x 0.0635 cm, Phifer©, Tuscaloosa, AL) was used to cover the top of the cages to prevent beetles from escaping. One hundred overwintering cages were built and placed in asparagus fields; 50 were placed in East Lansing, and the other 50 were placed in Hart. Each substrate treatment was replicated ten times at each location. Each substrate treatment was placed into an overwintering cage and evenly spread approximately 5cm thick, and then weighed on a scale to ensure a uniform density for each treatment. Ten common asparagus beetle adults, *Crioceris asparagi* (Coleoptera: Chrysomelidae) were placed into each overwintering cage.

Adult beetles were collected from commercial fields prior to overwintering throughout the last week of August and first week of September (2019). Adult beetles were collected by hand from asparagus fern and decomposing asparagus stalks found within asparagus fields located throughout Hart, MI and Dowagiac, MI, and then placed into plastic collection vials (5.72cm x 2.54cm, Thermo Scientific™ , Waltham, MA). Once collected, beetles were transported to the Michigan State University Greenhouses and kept in mesh enclosures (68.58cm x 68.58cm x 121.92, Nasco, Fort Atkinson, WI) between 20-27°C for 3 weeks. Inside the cages, fresh asparagus fern was kept in water, and water-soaked cotton balls were left in petri dishes at all times. Beetles were transported in small plastic containers (5.715cm x 2.54cm, Thermo Scientific™ , Waltham, MA) inside of a cooler to be placed into overwintering cages. Beetles were transferred from vials into overwintering cages in East Lansing, MI on September 20th, 2019 and in Hart, MI on September 30th 2019 and secured with the aluminum screening.

All overwintering cages were deconstructed in late February and March of 2020, with half of the cages removed on February 24th and the other half on March 22nd. Contents of each cage were placed into plastic bags and transported back to the laboratory. Samples were kept under refrigeration for one month at 4°C until assessment. Samples were kept at room temperature for at least 1 h prior to assessing beetle survival. Sample contents were placed onto a tray, and visually assessed for beetles. If beetles showed movement within 10-15 min of detection, beetles were counted as 'alive' or if they were immobile or missing body parts they were categorized and counted as 'dead'.

Tree surveys

To better understand whether various tree characteristics in woodlots surrounding asparagus fields impacted asparagus beetle abundance, tree surveys were conducted within woodlots parallel to asparagus fields that were previously surveyed for beetle populations. A starting point along the previously established 25m beetle population transects was selected randomly. A 2m wide transect was visually surveyed 10m into the woodlot from the woodlot edge (Fig. 2.3). Tree species, diameter at breast height (DBH), bark texture, and length within the transect was quantified. Only trees that were > 1.4m tall, with a circumference > 3cm, and with the whole trunk situated within the 2m wide transect were measured. Diameter at breast height was measured at 1.3m from the ground. Bark texture was visually rated using a scale with five different classes based on the thickness and texture of the bark (Table S2.2). Bark ratings ranged from 1-5, with lower ratings indicating smoother bark with less ridges and higher ratings demonstrating highly ridged, and sometimes peeling bark. The distance of each tree's location from the woodlot's edge was measured using a tape measure.

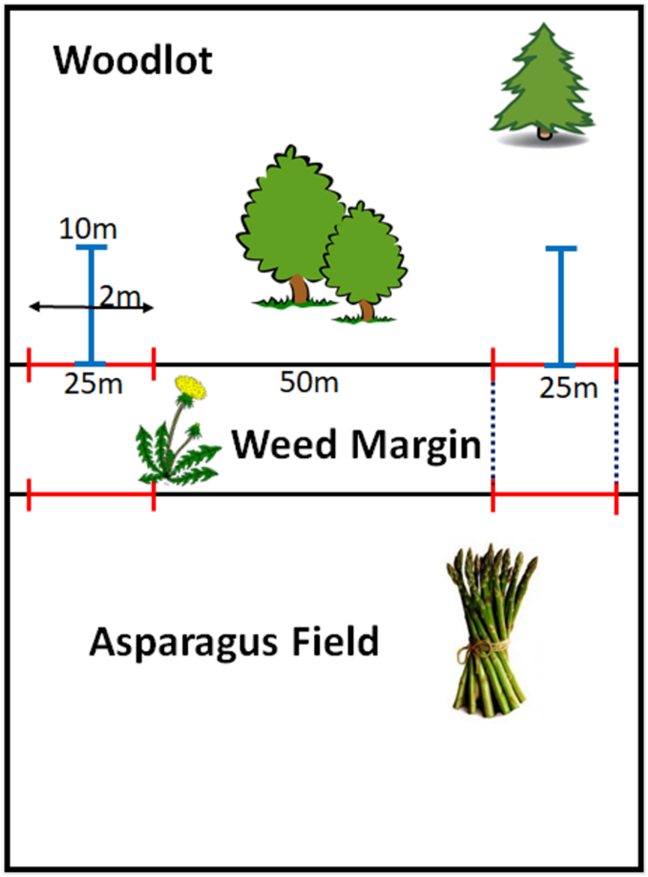

Figure 2.3 Tree surveys were conducted to determine the number of overwintering asparagus beetles in woodlots adjacent to commercial asparagus fields in Michigan in 2019-2020. Transects (25m long) along the border of woodlots were visually surveyed in August-September 2019 and July-September 2020. Red lines represent 25m transects conducted along asparagus field and woodlot edges. Each 25m transect was spaced 50m apart varying from 5-10 transects per field. Black dotted lines represent that both transects along asparagus fields and woodlots were parallel to each other. Blue lines represent the 10mx 2m transects perpendicular to the border of the woodlot to survey trees inside the woodlots.

Statistical analyses

Numbers of adult asparagus beetles in overwintering cages were analyzed using a mixed effects model with a 'Poisson' distribution GLMER (package = "LME4") with substrate as a fixed effect, and the location (East Lansing, MI or Hart, MI) as a random effect. Overwintering beetle ground cover data was analyzed similarly using a mixed effects model with a 'Poisson' distribution GLMER (package= "LME4") with the sampled habitat type as the fixed effect, and the field as a random effect. Two separate models were used with 'dead' beetles and 'alive' beetles as response variables. I checked for overdispersion in the models by using the 'dispersion_glmer' function (package= "blmeco"). An ANOVA test was used to compare models using the 'Anova' function in R version 3.6.1 (R core team, 2015). When the ANOVA results were significant, I conducted means comparisons using the 'emmeans' function (package = "emmeans").

To test the effect of tree characteristics throughout the surrounding semi-natural habitat, generalized linear mixed models were used with Template Model Builder (glmmTMB) and a negative binomial ("nbinom2") distribution. To determine which parameters should be included in the model, I used the 'dredge' function (package = "MuMIn"). Based on ΔAIC values produced by the 'dredge' function, the number of coniferous trees, number of dead trees, tree DBH, bark rating, and Shannon Diversity Index (SHDI) were used as fixed effects while field and transect were used as random effects in the best fitting model. To determine whether these measures were potentially correlated, I used a correlogram analysis (Fig. S2.2). I assessed the normality of each parameter and if parameters were correlated over 0.8 or under -0.8, they were removed from the model. The response variables were the total number of asparagus beetle eggs, larvae, and adults during the summer and fall. Data were standardized by scaling the log of model predictor variables.

Results

Summer and fall beetle surveys

Throughout August-September of 2019, 1,820 adult asparagus beetles, 1,857 asparagus beetle larvae, and 5,050 asparagus beetle eggs were observed along the edge of asparagus fields.

In July-September of 2020, 1,167 adult asparagus beetles, 2,027 asparagus beetle larvae, and 3,098 eggs were observed along the edge of asparagus fields.

Overwintering beetle sampling

In the winter of 2019-2020, 109 adult asparagus beetles were collected from 1m^2 quadrat samples in asparagus fields, weed margins, and woodlots. The majority of live beetles (N=9) were found overwintering within deciduous leaves, while a majority of dead beetles (N=10) were found overwintering in soil (Fig. S2.1). Habitat type affected asparagus beetle survival (χ^2=30.55, df=2, $P < 0.001$, Fig. 2.4A) and mortality (χ^2=15.95, df=2, $P < 0.001$, Fig. 2.4B). Overwintering asparagus beetle survival was significantly higher in asparagus fields than in woodlots (z > 5.53, df= 2, $P < 0.001$, Fig. 2.4A). Overwintering mortality was significantly higher in asparagus fields than in weed margins (z > 3.001, df= 2, $P < 0.001$, Fig. 2.4B) and woodlots (z > 2.79, df= 2, P< 0.001, Fig. 2.4B).

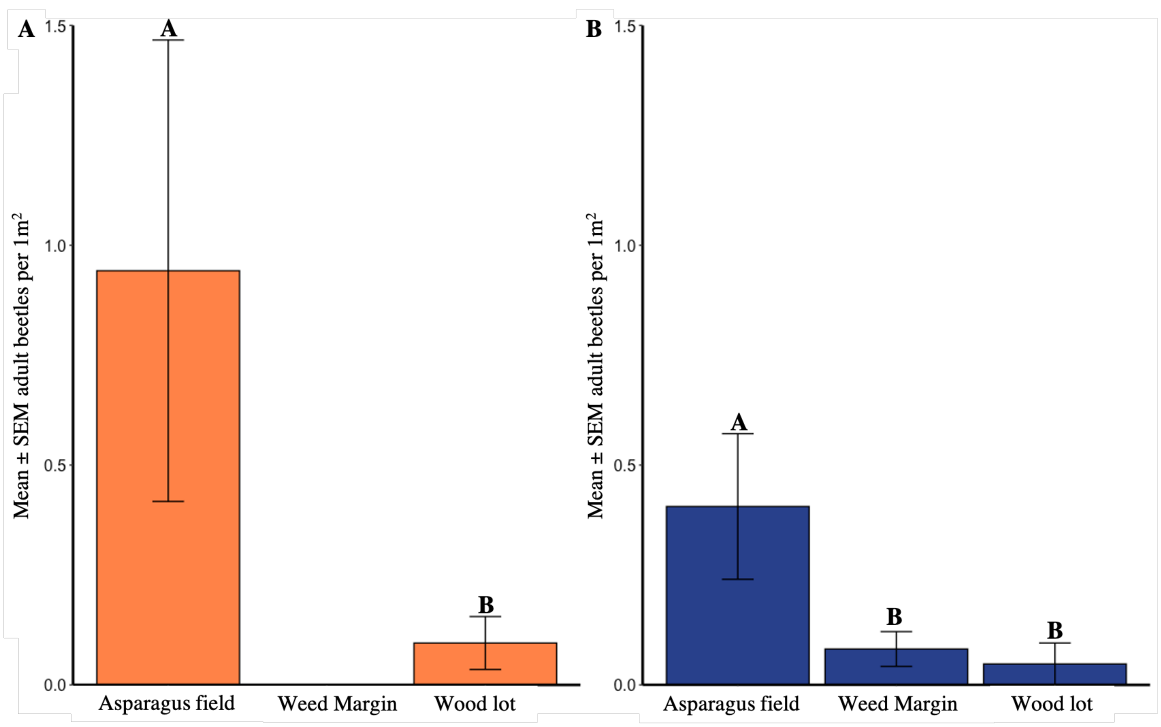

Figure 2.4 . Mean ± SEM overwintering adult asparagus beetle survival (A) and mortality (B) collected in quadrats by gathering litter from the soil surface in three different habitat types (see blue boxes in Fig. 2.1) in 2019-2020. Treatments with shared letters are not significantly different from one another (GLMM, p<0.001).

Overwintering cages

Survival of 517 adult asparagus beetles was assessed in 99 overwintering cages, 50 cages in Hart, MI (Oceana county) and 49 cages in East Lansing, MI (Ingham county) in 2019-2020. There was a significant substrate effect on asparagus beetle survival (χ^2=21.42, df=4, $P < 0.001$, Fig. 2.5A), but not on asparagus beetle mortality (Fig. 2.5B). Overwintering asparagus beetle survival was significantly higher in the cages containing deciduous leaves in comparison to coniferous leaves (z > -2.82, df=4, $P < 0.001$), thick bark (z > 3.37, df=4, $P < 0.01$) and thin bark (z > 3.84, df = 4, $P < 0.01$, Fig. 2.5A).

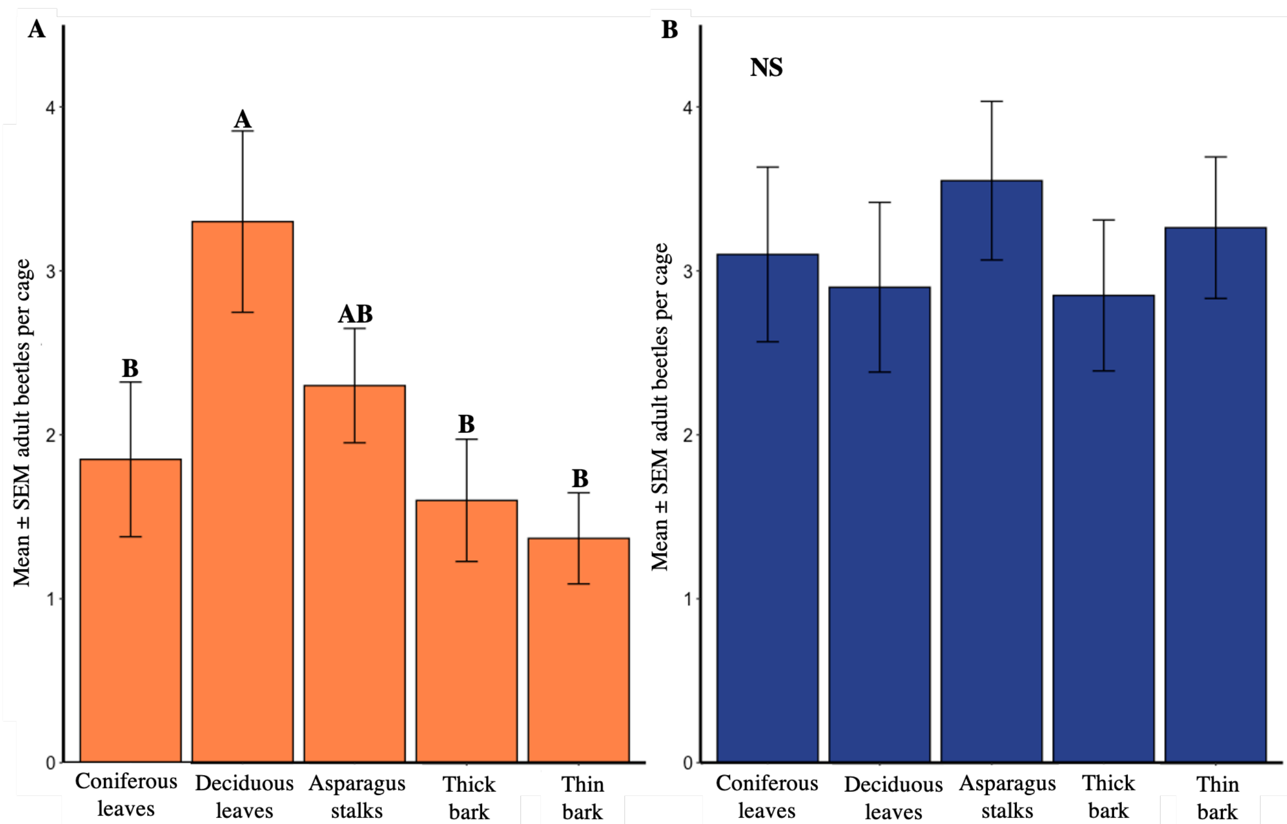

Figure 2.5 Mean ± SEM number of overwintering adult asparagus beetles that were placed in overwintering cages from October 2019 to March 2020 that survived (A) and died (B) per overwintering cage. Ten asparagus beetles were placed into each overwintering cage. Treatments with shared letters are not significantly different from one another (GLMM, p<0.01).

Tree surveys

In 2019-2020, 279 trees representing 34 species (Table S2.4) were recorded in transects in woodlots surrounding 11 commercial asparagus fields in Oceana and Cass Counties. I found that DBH, bark rating, coniferous trees, dead trees, and SHDI were not strongly correlated with one another, thus each of them could be potentially influencing total beetle abundance (Fig. S2.2). I found that none of these factors were strongly correlated with one another, thus each of them could be potentially influencing total beetle abundance. There was a negative relationship between the number of dead trees per transect and the total abundance of beetles per transect (z > -2.193, $P < 0.05$, Fig. 2.6; Table S2.3).

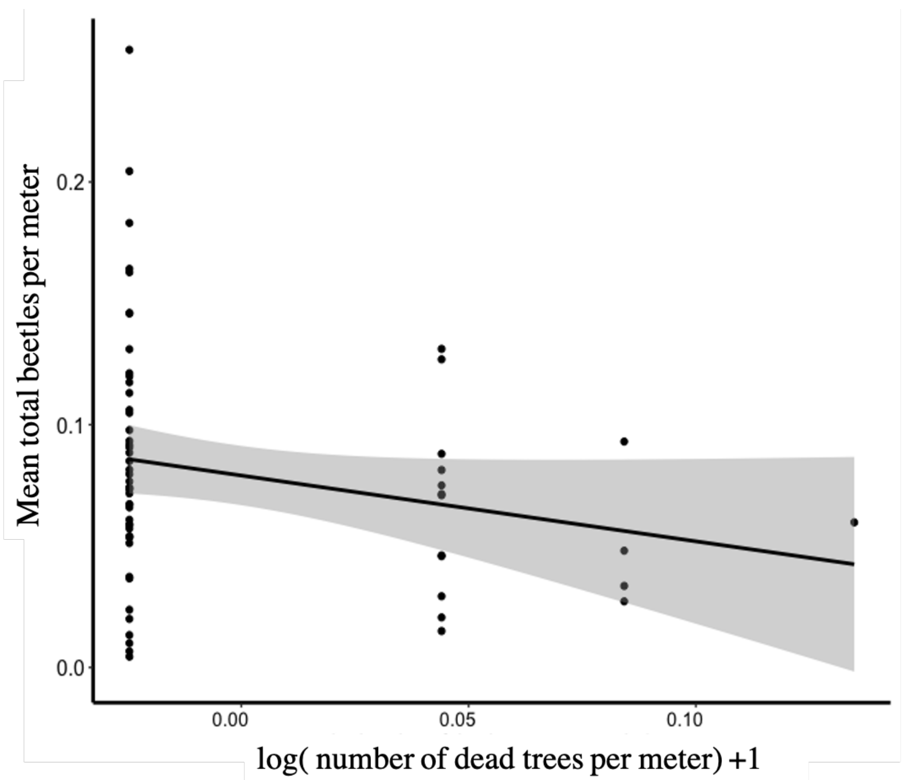

Figure 2.6. Relationship between mean total asparagus beetles observed along transects on the edge of asparagus fields and the number of dead trees found within surrounding non-crop habitat.

Discussion

Asparagus fields provide crucial overwintering habitat for asparagus beetles

I investigated the overwintering ecology of asparagus beetles and found that the majority of overwintering asparagus beetles were collected within asparagus fields in comparison to semi-natural habitats. This may be to minimize energy expenditure invested into locating distant overwintering sites, when suitable ones are readily available at their former feeding sites. Asparagus beetles also seem to survive at higher numbers within asparagus fields rather than surrounding habitats, which could be due to decreased predation (Ingrao et al. 2016).

Asparagus fields had about 23 times more overwintering beetles on average than field margins, and eight times more than woodlots as indicated by quadrat sampling. The landscape supplementation hypothesis (Dunning et al. 1992) may provide an explanation for asparagus beetles using all the examined habitats for overwintering at varying abundances. This hypothesis states that organisms within a population may supplement their resources by moving to the surrounding habitat when resources are limited, as long as the new habitat is within the organism's dispersal range. Thus, although most beetles are primarily utilizing overwintering habitat within the crop field itself, they could be using semi-natural habitats when overwintering habitats are limited within the field. Furthermore, asparagus beetle overwintering success was the highest for the deciduous leaf treatment. Deciduous leaves are oftentimes found within the asparagus fields, but if deciduous leaves are not present in the crop field, beetles are perhaps more likely to disperse throughout surrounding habitats to find more suitable overwintering substrates.

Survival of asparagus beetles throughout overwintering sites

Anecdotal evidence suggests that asparagus beetles can overwinter in various substrates such as decaying plant material (i.e., dead asparagus stalks and leaves), woody debris and loose bark (Chittenden 1917). However, a quantitative understanding of how these substrates impact asparagus beetle overwintering survival has not been considered previously. Based on my findings, asparagus beetles demonstrated the highest survival in overwintering cages when in the deciduous leaves treatment. Deciduous leaves provide thermal insulation for arthropods during extreme winter temperatures (Gallé et al. 2018, Maudsley et al. 2002). Since deciduous leaves in the winter are distributed throughout the habitat and are not exclusively found in the crop field, beetles can find this ground cover outside asparagus fields. Because most beetles remain within the crop field, it is likely that they prefer the overwintering sites found in asparagus fields. Beetles overwintering within asparagus stalks had an average of 1.5 times higher survival compared to the other tested substrates, although this was not statistically significant. Additionally, when sampling ground cover for overwintering beetles throughout habitat types, most live beetles were found in leaves or asparagus stalks. This demonstrates that both deciduous leaves and asparagus stalks could provide ideal overwintering sites for beetles, but the availability of deciduous leaves is dependent on the composition of the surrounding environment, while the availability of asparagus stalks is dependent on grower management. Based on this, mowing the stalks in the fall, prior to beetle overwintering, could mechanically break stalks down and lead to quicker decomposition, reducing the availability of suitable overwintering habitat.

Composition of surrounding semi-natural habitats

While these results suggest that asparagus beetles primarily overwinter within asparagus fields, the surrounding semi-natural habitats could still play a role in their overwintering. Specifically, access to deciduous leaves may be a key factor for the overwintering success of asparagus beetles. Although I did not identify a specific tree species that supports beetle overwintering, these findings indicate that dead trees and total beetle abundance are negatively correlated during the summer and fall. Thus, dead trees, which do not produce leaves in the fall, are likely contributing to overwintering mortality due to unsuitable overwintering habitat. Conversely, this finding could indicate the importance of tree health in surrounding non-crop habitat in relation to asparagus beetle abundance and should be further explored.

A recent review suggests that increasing semi-natural habitat could promote pest populations (Tscharntke et al. 2016). Specifically, semi-natural habitats may be acting as sources for pest populations at different life stages. Throughout a pest's development, habitat breadth can vary at different life stages. Generalist pests can persist on multiple resources both inside and outside crop fields, while specialists are less likely to be influenced by non-host resources in the environment. However, the availability of specific habitat for survival and reproduction (e.g., oviposition, overwintering) can impact specialist pest populations. For example, while the Mexican bean beetle (*Epilachna varivestis,* Coleoptera: Coccinellidae) prefers to reproduce within the crop field, it utilizes surrounding wooded edges as overwintering habitat (Stinner et al. 1982). Thus, dependency on different habitat types throughout an agroecosystem can change throughout a pest's lifecycle. Based on my findings, a majority of asparagus beetles are not utilizing non-crop habitats as overwintering habitat. However, they are dependent upon resources such as deciduous leaves that are originating from these non-crop habitats throughout overwintering. Further investigation of how the composition of different semi-natural habitat types is influencing asparagus beetle density is needed. In particular, future studies should focus on how the spatial distribution of deciduous trees, which seem to be important for asparagus beetle overwintering success, influence asparagus beetle population dynamics.

Conclusions

In conclusion, these findings demonstrated that asparagus beetles are primarily overwintering within asparagus fields rather than surrounding semi-natural habitats. While a majority of beetles are not utilizing surrounding habitats for overwintering, more beetles survive when using deciduous leaves that originate from surrounding trees as overwintering shelter. I also found that asparagus fields surrounded by more dead trees were correlated with lower abundances of active beetles during the summer and fall, possibly due to lack of deciduous leaves that fall into the crop field for overwintering habitat. Consequently, tree health within the surrounding non-crop habitat could be playing an important role in overwintering beetle survival. Ultimately, although the asparagus beetle is a specialist feeder and primarily utilizes the crop field, the surrounding environment could be influencing asparagus beetle overwintering success.

APPENDIX

Table S2.1 Study sites that were located in commercial asparagus used to survey asparagus beetle abundance and tree characteristics in surrounding semi-natural habitats during the growing season in 2019-2020. Site characteristics such as location, years sampled, crop field area (ha), the perimeter (km) of the field adjacent to semi-natural habitat (SNH), number of beetle and tree surveying transects, top three major tree species, and average tree Diameter at Breast Height (DBH) are included.

Site	Coordinates	County	Years	Field area	SNH pm	Transects	Major Trees	DBH
B_1	-86.393171, 43.797583	Oceana	2019-2020	10.58	0.13	5 *	*Elaeagnus umbellata* *Picea pungens* *Quercus rubra*	9.8
B_2	-86.384626, 43.801411	Oceana	2019-2020	12.1	1.11	7	*Acer saccharum* *Pinus strobus* *Quercus rubra*	18.1
AW_1	-86.423647, 43.715906	Oceana	2019-2020	4.88	0.69	8	*Acer nigrum* *Betula papyrifera* *Fraxinus americana*	12.5
AW_2	-86.438731, 43.693925	Oceana	2020	5.39	0.81	5	*Elaeagnus umbellata* *Prunus nigra* *Rhus typhina*	6.1
J_1	-86.177673, 43.618356	Oceana	2020	16.3	0.98	10	*Acer sp.* *Elaeagnus umbellata* *Pinus sylvestris*	15.5
V_1	-86.048926, 41.950965	Cass	2019	18.91	1.99	10	*Prunus serotina* *Prunus virginiana* *Sassafras albidum*	15.8
V_2	-86.036962, 41.951909	Cass	2019-2020	4.59	0.36	5	*Acer saccharum* *Robinia pseudoacacia* *Ailanthus altissima*	14.4
V_3	-86.128834, 41.973607	Cass	2019-2020	30.16	1.96	7	*Quercus rubra* *Rhus typhina* *Sassafras albidum*	6.9
V_H	-86.117048, 41.959539	Cass	2019-2020	9.89	0.57	7	*Prunus serotina* *Quercus rubra* *Sassafras albidum*	15.3

K_1	-86.306111, 42.135556	Cass	2020	3.42	0.33	5	*Prunus serotina* *Rhus typhina*	14.1
K_2	-86.302840, 42.136690	Cass	2020	6.05	0.39	5	*Gleditsia triacanthos* *Lonicera maacki* *Rhus typhina*	11.7

* 50m buffer transects were not used when surveying asparagus beetle abundance due to size

Table S2.2 Descriptions of bark rating scale used for classifying live tree bark.

Rating	Description
(1) Smooth adhered bark	Bark is smooth with little to no ridges; no open crevices; bark is tightly adhered to the trunk with no peeling
(2) Mostly smooth and mostly adhered bark	Bark is mostly smooth, but may have small ridges; infrequent open crevices; bark is mostly adhered to the trunk
(3) Slightly ridged and mostly adhered bark	Bark has frequent ridging; a moderate number of open crevices, bark is peeling off trunk in some places
(4) Moderately ridged and/or peeling bark	Bark has defined ridges; frequent open crevices; bark off trunk is frequently peeling
(5) Highly ridged and peeling bark	Majority of the bark is peeling off the trunk; many open crevices

Table S2.3 Model parameters and test statistics that were used for the analysis of the relationship of tree characteristics in surrounding semi-natural habitats and asparagus beetle abundance in asparagus fields surveyed in 2019-2020.

Parameter	Estimate	Std. Error	Z-value	P-value
Shannon index	-0.0432	0.0556	-0.777	0.4372
Coniferous trees	0.0773	0.0671	1.152	0.2494
Dead trees	-0.1387	0.0544	-2.549	0.0108*
Bark rating	0.0134	0.0776	0.173	0.8630
DBH	0.0449	0.0846	0.531	0.5952

* *P* value <0.05

Table S2.4 Number of trees recorded by species, bark rating, and DBH recorded in woodlots surrounding commercial asparagus fields.

Common Name	Scientific name	N	Bark rating	DBH
Black maple	*Acer nigrum*	6	2.5	19.18
Silver maple	*Acer saccharinum*	2	3.5	58.25
Sugar maple	*Acer saccharum*	17	1.47	11.97
-	*Acer sp.*	7	2.43	15.47
Tree of heaven	*Ailanthus altissima*	2	1	8.25
Yellow birch	*Betula alleghaniensis*	3	2	3.39
Paper birch	*Betula papyrifera*	2	3	28.97
-	*Betula sp.*	1	1	2.5
Common hackberry	*Celtis occidentalis*	3	2	13.35
Flowering dogwood	*Cornus florida*	1	3	18.15
Autumn olive	*Elaeagnus umbellata*	17	1.24	3.39
White ash	*Fraxinus americana*	2	2	2.5
Green ash	*Fraxinus pennsylvanica*	1	2	21.09
Honey locust	*Gleditsia triacanthos*	3	2	21.63
Eastern red cedar	*Juniperus virginiana*	1	1	-
Amur honeysuckle	*Lonicera maackii*	4	1	1.5
-	*Lonicera sp.*	3	1	1.84
Sweet crabapple	*Malus coronaria*	2	5	19
White mulberry	*Morus alba*	2	2	11.75
American hophornbeam	*Ostrya virginiana*	1	5	9.24
Blue spruce *	*Picea pungens*	10	3	11.45
Eastern white pine *	*Pinus strobus*	8	3	33.52
Scots pine *	*Pinus sylvestris*	19	2.32	-
Quaking aspen	*Populus tremloides*	1	1	7.32
Canada plum	*Prunus nigra*	1	3	6.17
Fire cherry	*Prunus pensylvanica*	1	4	24.8
Black cherry	*Prunus serotina*	31	3.71	25.14
Chokecherry	*Prunus virginiana*	7	2.14	12.36
-	*Prunus sp.*	1	3	31
Swamp white oak	*Quercus bicolor*	1	1	2.23
Bur oak	*Quercus macrocarpa*	1	2	3.82
Red oak	*Quercus rubra*	16	1.56	12.24
Black oak	*Quercus velutina*	1	2	14.5
Common buckthorn	*Rhamnus cathartica*	2	2	3.25
Staghorn sumac	*Rhus typhina*	24	1.38	5.27
Black locust	*Robinia pseudoacacia*	4	3	25.72
Sassafras	*Sassafras albidum*	33	2	5.38
Eastern hemlock *	*Tsuga canadensis*	2	2	7.95
Slippery elm	*Ulmus rubra*	4	1.8	2.6
Rock elm	*Ulmus thomasii*	1	2	9.3
Nannyberry	*Viburnum lentago*	1	2	-
-	*Unidentified*	30	3.7	5.72
Total	**30**	**174**		

Note: Species marked with an asterisk (*) indicate coniferous tree species.

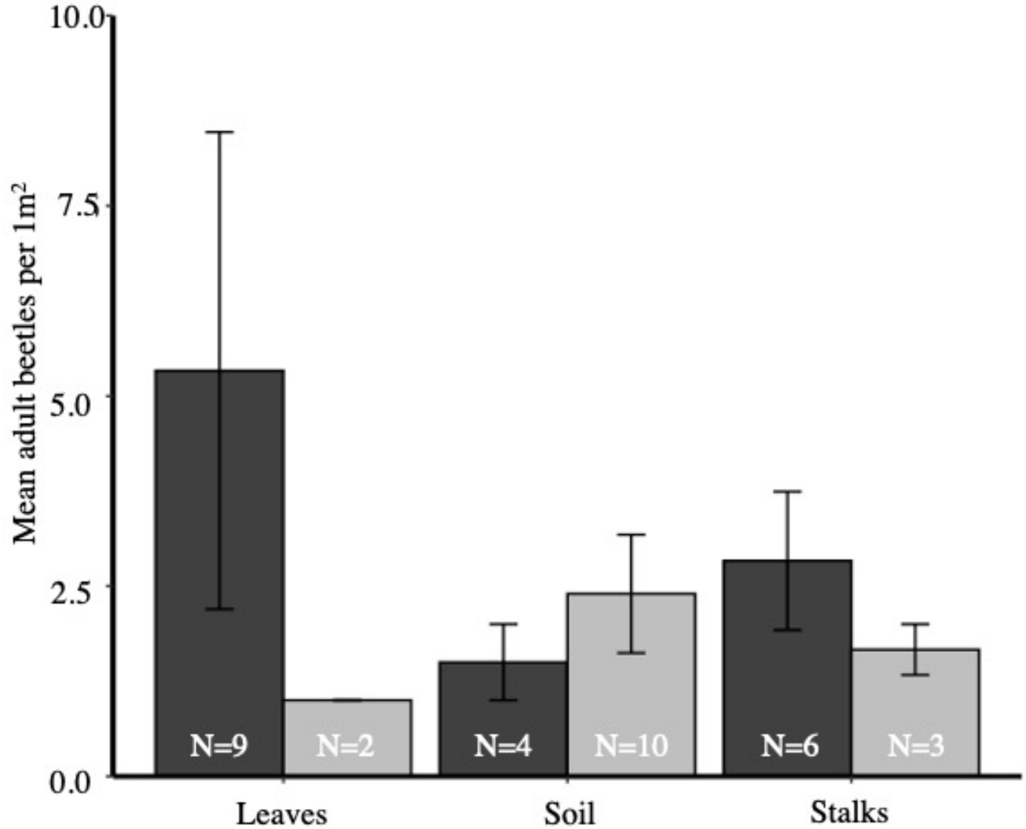

Figure S2.1 Mean ± SEM number of overwintering adult asparagus beetles that were collected in substrates by gathering litter from soil surface in all three different habitat types (see blue boxes in Fig. 2.1) that were alive (dark grey bars) and dead (light grey bars) in 2019-2020.

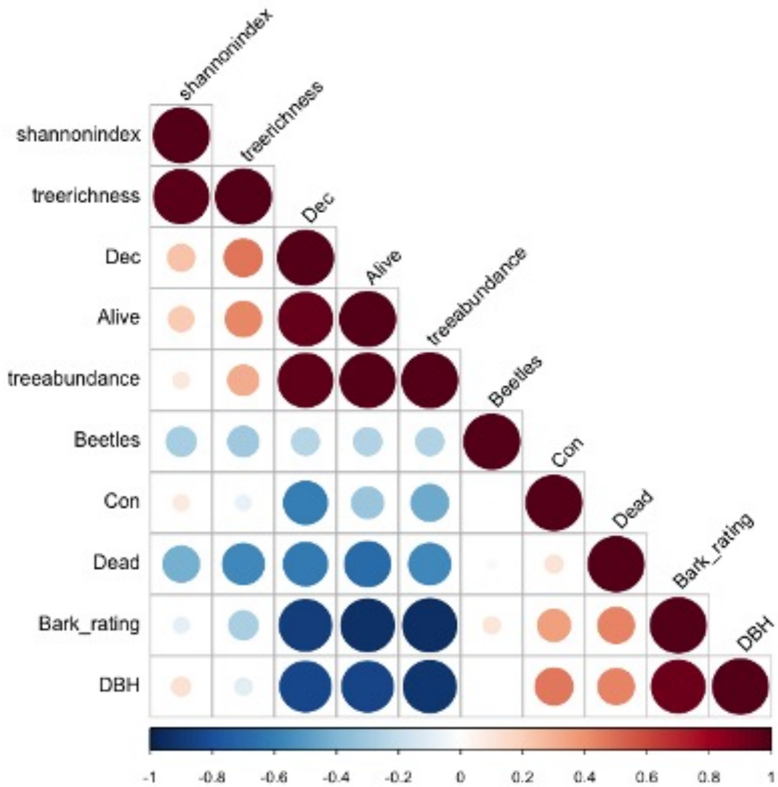

Figure S2.2 A correlogram comparing correlations between model parameters used in a global model to determine whether there is a relationship between total asparagus beetle abundance in commercial asparagus fields and tree characteristics within surrounding non-crop habitat. Model parameters included Shannon Diversity Index (shannonindex), tree richness (treerichness), number of deciduous trees (Dec), number of live trees (alive), tree abundance (treeabundance), total beetles (Beetles), number of coniferous trees (Con), number of dead trees (Dead), bark rating (Bark_rating), and Diameter at Breast Height (DBH). Positive correlations are displayed in red and negative correlations in red color. Color intensity and the size of the circle are proportional to the correlation coefficients.

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CHAPTER 3:

Landscape composition and configuration influence the abundance of *Crioceris asparagi* in asparagus agroecosystems

Introduction

Management of arthropod pests has often been focused on the crop field, frequently relying on the application of insecticides and other within-field management strategies. However, the surrounding landscape can also play a major role in pest suppression of cropping systems. Restructuring landscape variables has been shown to influence both pest and natural enemy population dynamics (Jonsson et al. 2010). The structure of landscape consists of two components: landscape composition and landscape configuration. Landscape composition refers to the proportion and diversity of land cover, while landscape configuration applies to the spatial arrangement (Fahrig et al. 2011).

Landscape composition can influence pest populations by impacting dispersal, mortality and reproduction (Veres et al. 2011). Landscape complexity increases with higher proportions of semi-natural habitat (e.g., forests, grassland) while pest abundance often declines or remains unchanged (Bianchi et al. 2006, Chaplin-Kramer et al. 2011). It has been suggested that these declines are a result of increased natural enemy populations due to the additional resources provided by these semi-natural habitats (Thies and Tscharntke 1999, Corbett and Rosenheim 1996). However, pest populations may actually increase when surrounding landscapes are more complex due to additional resource availability for insect pests as well (Tscharntke et al. 2016). For instance, in Chapter 2, I found that asparagus beetles utilize both surrounding woodlots and field margins as overwintering habitat. Although a majority of beetles were found in asparagus fields, beetles were still present in surrounding semi-natural habitats. In fact, asparagus beetles contained in cages with various substrates (tree bark, coniferous leaves) survived at higher rates when deciduous leaves were present. Consequently, it is evident that this specialist pest is utilizing resources found outside of the field to increase its success. Based on these findings, I was interested to determine how the abundance of asparagus beetles, a pest that primarily relies crop habitat, yet utilizes semi-natural habitat resources, would be impacted by the proportion of different land covers in the greater landscape.

While there has not been previous research looking at the influence of landscape variables on asparagus beetles, prior studies have found that insect herbivores can respond differently to the landscape at varying spatial scales (Jonsen and Fahrig 1997). For instance, the codling moth (*Cyrdia pomonella* L., Lepidoptera: Tortricidae), a specialist pest, was found to only be influenced by landscape variables at distances lower than 150m, indicating that management should be focused within the field's vicinity (Ricci et al. 2009). In winter oilseed rape, pod midges (*Dasineura brassicae* Winn, Diptera: Cecidomyiidae) and stem weevils (*Ceutorhynchus napi* Gyll., Coleoptera: Curculionidae) only respond to landscape variables at small (250-500m) and medium scales (1000-1250m), while pollen beetles (*Meligethes aeneus* Fabr. Coleoptera: Nitidulidae) respond at larger scales (100-2000m) (Zaller et al. 2008). Ultimately, an understanding of how an insect pest like the asparagus beetle is affected by the landscape at different scales could suggest its dispersal and potential management area.

Although numerous studies have suggested that landscape composition can be highly influential on pest abundance, landscape configuration is proving to be an important factor as well. Landscape configuration may have a larger effect on arthropods in comparison to composition (Zhang et al. 2020, Martin et al. 2019). One measure of configuration that has been commonly used to better understand arthropod population dynamics is edge density. Edge density refers to the sum of the lengths of all edge segments in a landscape in relation to the total landscape area. Based on the 'landscape complementation hypothesis', some arthropods will use resources from different types of land cover at different life stages (Dunning et al. 1992). Asparagus beetles may rely on resources from surrounding semi-natural habitats for their overwintering success thus if the edge density of landscape is higher, they likely spill over from surrounding land covers. Another measure of configuration commonly used is the diversity and evenness of land cover types in a landscape, or Shannon's Diversity Index (SHDI). More diverse landscapes support higher populations of beneficial arthropods and increase ecosystem services (Bianchi et al. 2006, Werling and Gratton 2008). Consequently, more diverse landscapes can promote pest suppression through natural enemies. However, the direct effect of high landscape diversity on asparagus beetle populations has not been explored.

The objective for this study was to understand how surrounding landscape composition and configuration influence asparagus beetle population abundance at various spatial scales. Consequently, I investigated the effect of landscape composition on asparagus beetles for the proportions of the following land covers that are dominant in the study region: asparagus, deciduous forest, evergreen forest and grassland/pasture. I also chose two measures of landscape configuration to explore- Shannon's Diversity Index (SHDI) and edge density. In terms of landscape composition, I hypothesized that more complex landscapes with higher proportions of semi-natural habitat would host a higher abundance of asparagus beetles. In particular, based on my previous findings reported in Chapter 2, I expected that there would be a positive relationship between asparagus beetle abundance and the proportion of deciduous forest within the landscape. Regarding landscape configuration, I hypothesized that landscapes with lower diversity or higher edge density would support more asparagus beetles. Furthermore, I decided to explore how asparagus beetle abundance was influenced based on the spatial scale of each landscape variable. I did this to learn more about how asparagus beetles respond to the resources present across farm landscapes.

Materials and Methods

Study site and experimental design

The study was carried out in the Midwest region of the United States in mid-western and southwestern regions of Michigan's lower peninsula (Fig. 3.1a). Research sites were in Oceana county in the northwest region and Cass county in the southwest region. These landscapes are characterized by small fragments of semi-natural habitats interspersed in agroecosystems. In Oceana county, the landscape is dominated by semi-natural habitat, consisting of deciduous forest (35%), woody wetlands (14%), corn (7%), evergreen forest (6%), cherries (5%), and other specialty crops and non-crop habitat. In Cass county, the landscape is more interspersed with field crops and semi-natural habitat, consisting of corn (23%), deciduous forest (21%), woody wetlands (16%), soybeans (15%), and other crops (NASS CDL 2020). A set of 11 asparagus fields (Fig. 3.1b, c) were selected over 2 years (7 fields in 2019; 10 fields in 2020). These fields were chosen based on their differences in surrounding land cover throughout asparagus producing regions. All asparagus fields used in this study were managed by growers and were sprayed with conventional insecticides as needed. I spaced out beetle surveying by at least a few days before or after each spray application.

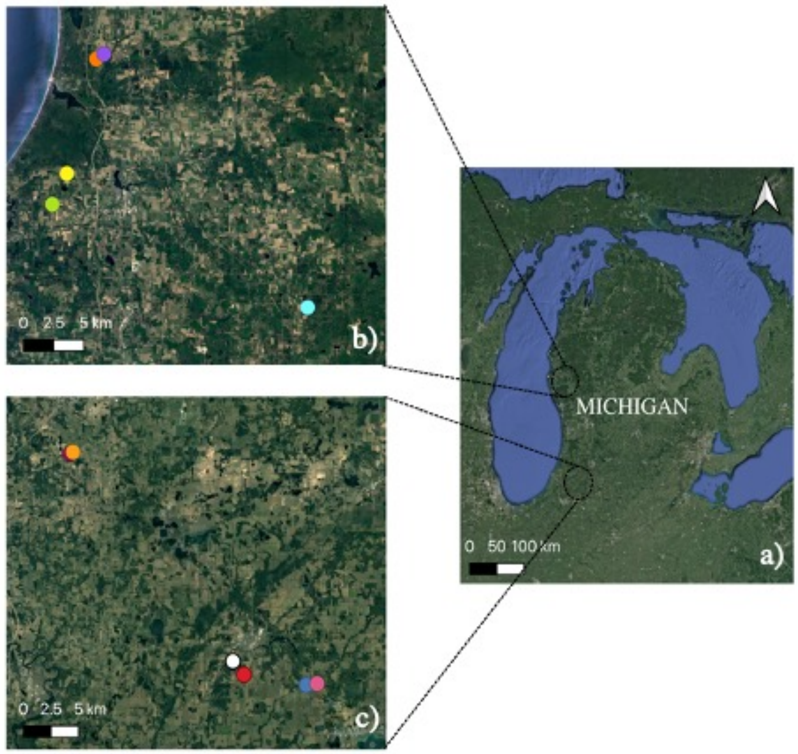

Figure 3.1 Location of the a) study area (Michigan, USA) and spatial distribution of the eleven asparagus fields (seven used in 2019 and ten used in 2020) in b) Oceana county, MI and c) Cass county, MI. Sample sites are represented by the colored circles. Each site was sampled for asparagus beetle abundance 2-3 times annually during the summers of 2019 and 2020. Land cover classifications were derived for the proportions of asparagus, deciduous forest, evergreen forest, grassland/pasture, Shannon's Diversity Index (SHDI), and edge density from the United States Department of Agriculture's National Agricultural Statistics Service Cropland Data Later for each year.

Asparagus beetle sampling

To measure the abundance of asparagus beetle populations throughout the growing season, commercial asparagus fields were surveyed using transects along the edge of commercial asparagus fields. In 2019, 7 fields were surveyed 3 times from August 7th to September 6th. In 2020, 10 fields were surveyed 2-3 times from July 21st to September 25th. Transects (25 m x 2 m) were established along the edge of asparagus fields that were bordered by woodlots. Between each transect a 50m buffer was created, with the exception of one smaller field. I walked the length of each transect and I visually surveyed the side of the asparagus plant within the transect that was towards the exterior of the field towards the woods. The number of transects varied between each field based on the area of the asparagus field (Table S2.1).

Landscape metrics

The influence of landscape composition and configuration on total asparagus beetle abundance was evaluated at different spatial scales. Land cover classifications surrounding each site were derived from the United States Department of Agriculture's National Agricultural Statistics Service Cropland Data Layer for 2019 and 2020 (NASS 2019-2020). Shapefiles were created based on the coordinates of each site in R studio (Version 1.3.1093). Buffers were created at varying spatial scales around the focal field (100, 200, 300, 400, 500, 750, 1000, 1250, 1500, 2000 m) and then raster files were created by clipping the areas of interest. For each buffer, the proportions of deciduous forest, asparagus, evergreen forest, and grassland/pasture were quantified around each asparagus field. Additionally, landscape configuration metrics such as Shannon's Diversity Index (SHDI) and edge density were calculated for each of these buffers using the 'landscape metrics' package in R studio (Version 1.3.1093). Shannon's Diversity Index is a diversity metric that takes into account both the number of classes and abundance of each class (Shannon and Weaver 1949). The edge density represents all the edges in the landscape in relation to the landscape area and was calculated by dividing the total landscape edge by the total landscape area (McGarigal et al. 2012). Due to variation of land cover classes present between years, I included 'Christmas trees' in the 'Evergreen forest' land cover class to maintain consistency.

Statistical analyses

To examine the effects of landscape parameters at varying spatial scales on asparagus beetle observations, I used a generalized linear model (GLM) with a negative binomial distribution. The distribution was selected based on the residuals and overdispersion of the model. The response variable was the total number of beetles (all life stages) measured per site. For each model, the proportion of either asparagus, deciduous forest, evergreen forest, or grass/pasture was used as a fixed effect and site was used as a random effect. Landscape variables were scaled to improve the fit of each model and normalize the data. Models were selected based on Akaike Information Criterion (AIC) values; the model with the lowest AIC was selected as the best fitting model for that spatial scale. To compare how the relationship between asparagus beetle abundance and different landscape parameters varied between spatial scales, z-values were used. For each z-score, an arbitrary threshold of above 2 or below -2 was used to indicate the significant effect of each landscape parameter on asparagus beetle abundance . Positive z-values indicate a positive relationship between beetle abundance and the landscape parameter, while negative z-values signify a negative relationship. The higher the positive value, the stronger the relationship is between beetle abundance and the landscape parameter. Similarly, lower negative z-values indicate a stronger negative relationship. Both asparagus beetle abundance and landscape parameter data was merged for 2019-2020, but analyzed combined and separately by county.

Results

Asparagus beetle abundance

Throughout August-September 2019, 1,820 adult asparagus beetles, 1,857 asparagus beetle larvae, and 5,050 asparagus beetle eggs were observed along the edge of asparagus fields (8,727 total). In July-September 2020 1,167 adult asparagus beetles, 2,027 asparagus beetle larvae, and 3,098 eggs were observed along the edge of asparagus fields (6,292 total

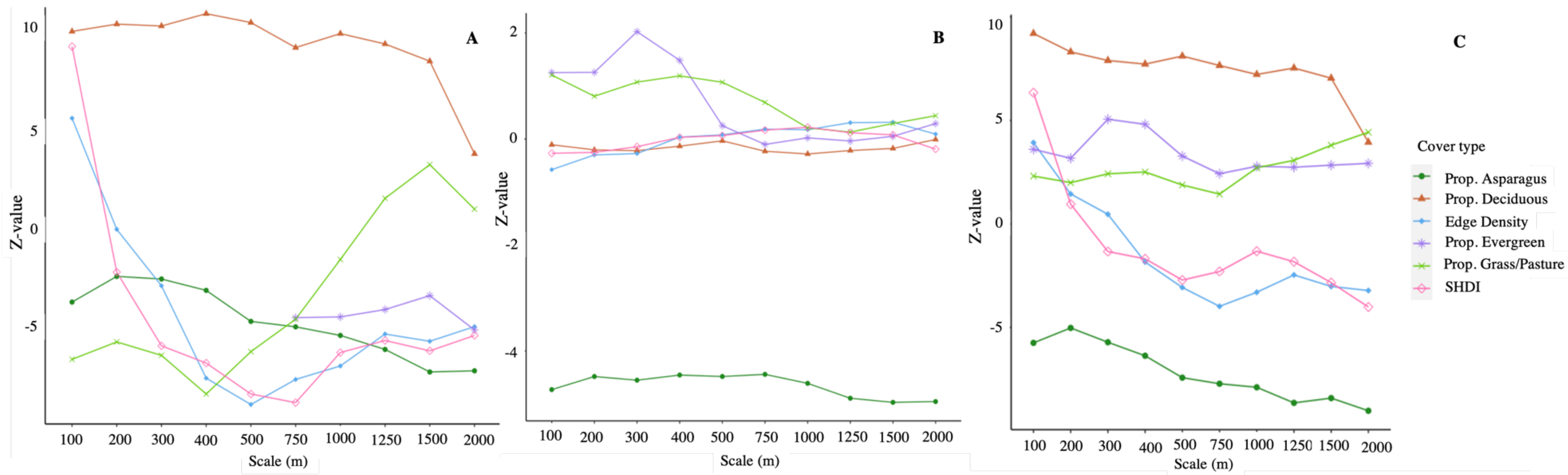

Figure 3.2 Z-values of each predictor at each scale for total asparagus beetle abundance calculated from the summary statistics of the generalized linear models (with a negative binomial distribution) for Cass county, MI (A), Oceana county, MI (B), and combined counties (C). Colors and symbols refer to various landscape variables. Z-values were calculated from the model summary for each landscape parameter at each spatial scale. No z-values were calculated for evergreen forest (100-500 m)in Cass County due to the absence of evergreen forest.

Landscape metrics throughout spatial scales

Cass County

In Cass County, the z-values of the proportion of deciduous forest ranged from 3.88 to 11.01 (Fig. 3.2 A). With the highest z-value at 100m (z-value = 11.01), the positive effect of the proportion of deciduous trees on total asparagus beetle abundance was the highest at lower scales and decreased as the spatial scale increased with the lowest effect at 2000m (z-value = 3.88). The z-values for the relationship between total beetle abundance and proportion of asparagus ranged from -7.23 to -2.36 (Fig. 3.2A). The effect of the proportion of asparagus on beetle abundance was less negative at 200m (z-value = -2.36) and was more negative as the spatial scale increased to 2000m (z-value = -7.17). In terms of Shannon's Diversity Index (SHDI), a strong positive effect was demonstrated at 100m (z-value = 9.34), but then became a negative effect on beetle abundance at higher spatial scales with the lowest value at 750m (z-value = -8.79). Similarly, edge density had a strong positive effect on beetle abundance at lower spatial scales (100m: z = 5.69) that became a negative effect at higher scales with the strongest negative effect at 500m (z-value = -8.89). The effect of the proportion of grassland on total beetle abundance was negative from 100-1000m (Fig. 3.2A) and became positive at higher spatial scales, peaking at 1500m (z-value = 3.33). Due to the absence of evergreen forest at lower spatial scales (100-500m), the effect of the proportion of evergreen forest was only observed for higher spatial scales (750-2000m). Consequently, there was a negative effect of the proportion of evergreen forest on total beetle abundance ranging from -3.34 to -5.09 (Fig. 3.2A).

Oceana County

In Oceana County, the proportion of asparagus had a consistent negative effect on the total asparagus beetle abundance with z-values ranging from -4.44 to -4.97 (Fig. 3.2B). The remaining landscape parameters had no effect on total asparagus beetle abundance falling under the threshold of 2, with the exception of the proportion of evergreen forest on total beetle abundance at 300m (z-value = 2.03).

Combined Counties

Z-values indicated that deciduous forest mediated beetle abundance overall. Deciduous forests had a positive effect on asparagus beetle abundance (z-values: 3.95 to 9.2, mean= 6.87; sd=1.51) with values highest at 100m (z-value = 9.2) and declining to 3.95 at 2000m. Overall, asparagus in the landscape had a negative effect on beetle abundance (z-values: -9.018 to -5.019, mean=-4.48; sd=0.86). At 100m, the z-value was at -5.02 and continued to decline as the scale increased to -9.02 at 2000m. Proportion of evergreen forest also positively influenced beetle abundance ranged (z-values: 2.43 to 5.06 (mean= 3.797; sd=0.607) with values staying consistent for 100m, 200m, and between 500m to 2000m (Table S3.2) but increasing between 300 and 400m to 4.81. All z-values, however, were above a threshold of 2 indicating that evergreen forest influenced beetle abundance at all spatial scales. The proportion of grassland/pasture in the landscape around focal asparagus fields also positively influenced beetle abundance, in general the influence of this parameter gradually increased with distance (z-values: 2.31 to 3.8, mean=3.07; sd= 1.11). At lower scales, the z-values are shown to be above the threshold of 2, but then fell below the threshold from 500-750m, and then increased above the threshold for the remaining larger scales. The Shannon's Diversity Index ranged from -4.01 to 6.34 (mean=-0.82; sd=2.75) with a positive effect close to focal asparagus fields (100m) but this gradually changed to a negative effect with increasing scale, starting at 300m. Edge density demonstrated a similar trend as SHDI, with the z-values ranging from -3.98 to 3.93 (mean= -1.14; sd= 2.50). Edge density had a positive effect on beetle abundance at close spatial scales but this gradually became a negative effect as scale increased. Ultimately, the proportion of deciduous forest had the highest z-values (mean= 6.87; sd=1.51) followed by evergreen forest (mean= 3.8; sd=0.61) and grassland/pasture (mean=3.07; sd= 1.11). On average, SHDI and edge density had z-values near zero (SHDI: mean = -0.82; Edge density: mean= -1.14). Lowest z-values were found for the proportion asparagus with a mean of -4.48.

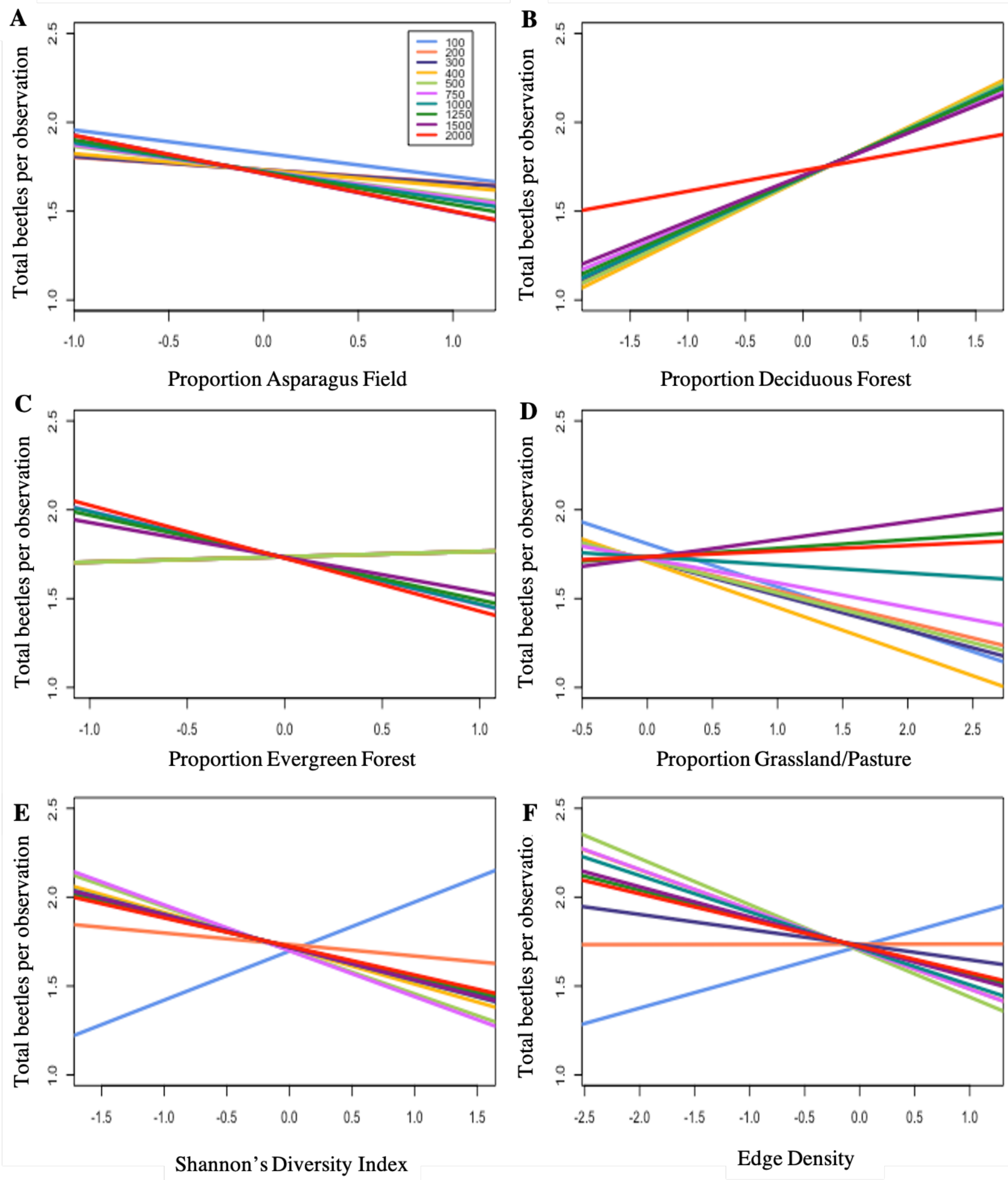

Figure 3.3 Relationships between the total abundance of asparagus beetles per observation and the proportion of parameters of landscape composition and configuration; (A) proportion of asparagus field, (B) proportion of deciduous forest, (C) proportion of evergreen forest, (D) proportion of grassland/pasture, (E) Shannon's Diversity Index (SHDI), and (F) edge density. Beetle abundance and landscape data was combined for 2019-2020 in Cass County. X-axis represents the proportion of land cover for each spatial scale (A-D) or the value of land cover diversity and evenness (E), or the number of edges within each spatial scale (F). Y-axis shows the mean total beetles that were counted per observation when surveying asparagus beetles along the edge of commercial asparagus fields. Colors represent different spatial scales. All landscape parameters were scaled. *See* Table S3.1 and S3.2 for summary statistics for combined counties.

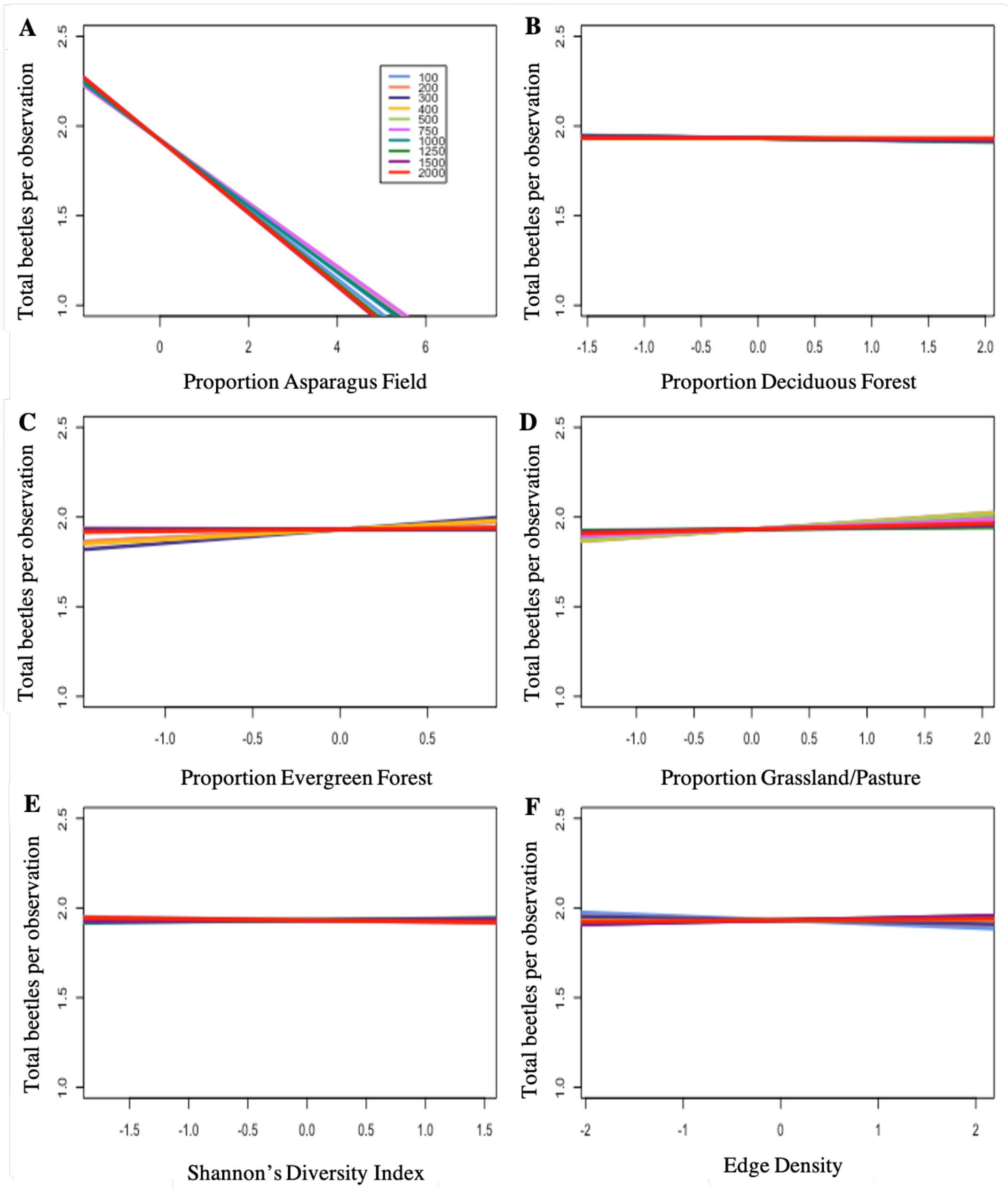

Figure 3.4 Relationships between the total abundance of asparagus beetles per observation and the proportion of parameters of landscape composition and configuration; (A) proportion of asparagus field, (B) proportion of deciduous forest, (C) proportion of evergreen forest, (D) proportion of grassland/pasture, (E) Shannon's Diversity Index (SHDI), and (F) edge density. Beetle abundance and landscape data was combined for 2019-2020 in Oceana County. X-axis represents the proportion of land cover for each spatial scale (A-D) or the value of land cover diversity and evenness (E), or the number of edges within each spatial scale (F). Y-axis shows the mean total beetles that were counted per observation when surveying asparagus beetles along the edge of commercial asparagus fields. Colors represent different spatial scales. All landscape parameters were scaled. *See* Table S3.1 and S3.2 for summary statistics for combined counties.

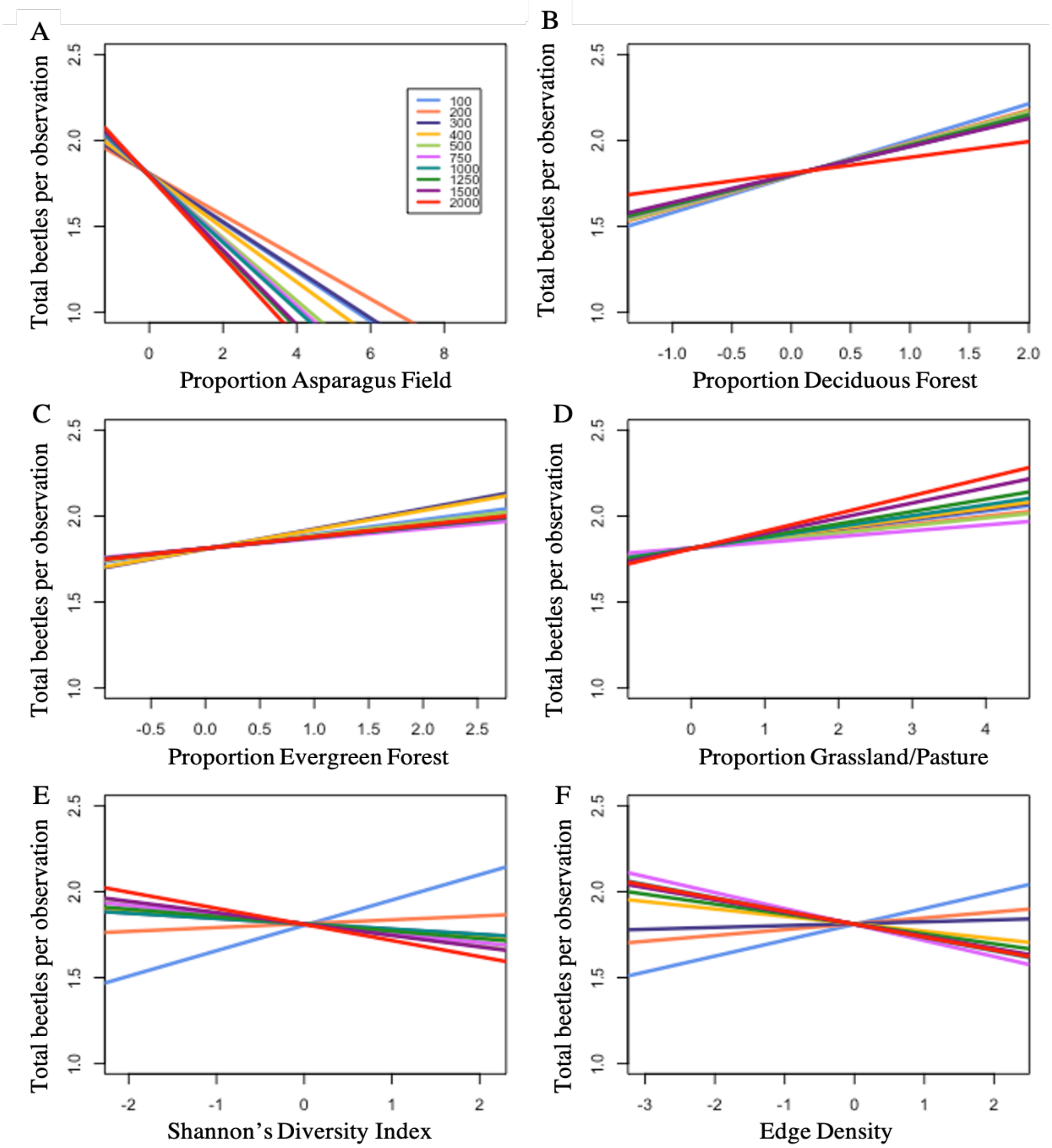

Figure 3.5 Relationships between the total abundance of asparagus beetles per observation and the proportion of parameters of landscape composition and configuration; (A) proportion of asparagus field, (B) proportion of deciduous forest, (C) proportion of evergreen forest, (D) proportion of grassland/pasture, (E) Shannon's Diversity Index (SHDI), and (F) edge density. Beetle abundance and landscape data was combined for 2019-2020 for both Cass and Oceana Counties. X-axis represents the proportion of land cover for each spatial scale (A-D) or the value of land cover diversity and evenness (E), or the number of edges within each spatial scale (F). Y-axis shows the mean total beetles that were counted per observation when surveying asparagus beetles along the edge of commercial asparagus fields. Colors represent different spatial scales. All landscape parameters were scaled. *See* Table S3.1 and S3.2 for summary statistics for combined counties.

Effects of landscape on pest abundance

Cass County

In Cass County, there was a negative relationship between total beetle abundance and the proportion of asparagus at all spatial scales, with the lowest estimate at 200m and the highest at 1500m (Fig. 3.3A, 200m: estimate = -0.07, se = 0.03, z = -2.36, P= <0.001; 1500m: estimate = -0.21, se = 0.03, z = -7.23, P = <0.001). The number of total beetles per observation was positively related to the proportion of deciduous forest, with the highest estimate at 400m (Fig. 3.3B, 400m: estimate = 0.32, se = 0.03, z= 11.01, P = <0.001). The proportion of evergreen forest had a negative relationship with total beetle abundance for spatial scales 750-2000m, with evergreen forest absent for lower scales (Fig. 3.3C). The proportion of grassland/pasture had a negative relationship with beetle abundance from 100-750m, with the highest estimate at 400m (Fig 3.3D, 400m: estimate = - 0.26, se = 0.03, z= -8.35, P = <0.001). From 1000-2000m, there was no relationship between proportion of grassland/pasture and beetle abundance (Fig. 3.3D). Edge density showed a negative relationship with total beetle abundance for all spatial scales except 200m (Fig. 3.3E, 200m: estimate = 0.001, se = 0.03, z = 0.03, P = 0.9). Shannon's Diversity Index demonstrated a negative relationship with total asparagus beetle abundance, with the exception of 100m. (Fig. 3.3F, 100m: estimate = 0.28, se = 0.03, z = 9.34, P = <0.001).

Oceana County

In Oceana County, there was a negative relationship between proportion of asparagus and total beetle abundance at all spatial scales, with the highest estimate at 1500m (Fig. 3.4A, 1500m: estimate = -0.2, se= 0.04, z = -4.97, P = <0.001). Total asparagus beetle abundance had no relationship with the remaining landscape parameters (Fig. 3.4B-F).

Combined Counties

There was a negative relationship between total beetle abundance and the proportion of asparagus at all spatial scales, with the lowest estimate at 200m and the highest at 2000m (Fig. 3.5A, 200m: estimate = -0.12, se = 0.024, z = -5.02, *P*= <0.001; 2000m: estimate = -0.23, se = 0.026, z = -9.02, *P* = <0.001). The number of total beetles per observation was positively related to the proportion of deciduous forest, with the lowest estimate at 2000m (Fig. 3.5B, estimate = 0.09, se = 0.023, z = 3.95, *P* = <0.001). The proportion of evergreen forest demonstrated a positive relationship with total beetle abundance throughout all spatial scales (Fig. 3.5C). The proportion of grassland/pasture demonstrated a positive relationship at lower scales (Fig. 3.5D, 100-400m, Table S3.1). From 500-750m, beetle abundance was not affected by grassland/pasture (500m: estimate = 0.04, se = 0.023, z = 1.88, *P* = 0.06; 750m: estimate = 0.03, se = 0.023, z = 1.44, *P* = 0.15), but then there was a positive relationship at larger scales (1000-2000m, Table S3.1). Edge density showed a positive relationship with total beetle abundance for smaller scales such as 100-200m (Fig 3.5E, 100m: estimate = 0.09, se = 0.024, z = 3.93, *P* = <0.001; 200m: estimate = 0.03, se = 0.024, z = 1.45, *P* = 0.001) and negative relationship at greater scales (500-2000m, Table S3.1). Between 300 and 400m, beetle abundance was not influenced by edge density (300m: estimate = 0.01, se = 0.023, z = 0.47, *P* = 0.64; 400m: estimate = -0.04, se = 0.023, z = -1.84, *P* = 0.066). Shannon's Diversity Index was positively related to beetle abundance at 100m (Fig. 3.5F,100m: estimate= 0.15, se = 0.023, z = 6.34, *P* = <0.001) and negatively related at the remaining higher scales (500-750m;1500-2000m, Table S3.1).

Discussion

My results indicated that asparagus beetle abundance was influenced by both landscape composition and landscape configuration. The influence of these factors on beetle abundance varied by distance from the field (scale) and between location. Both counties demonstrated a compelling result- the importance of the proportion of asparagus fields on asparagus beetle abundance. To my surprise, asparagus beetle abundance declined as the proportion of asparagus fields increased in the landscape. This finding demonstrates the importance of semi-natural habitat to asparagus beetle abundance, showing an opposite trend. Although asparagus beetles are dependent upon the crop field for foraging and reproduction, their overwintering success, which is dependent upon deciduous leaves, may be the most critical factor to their abundance. Z-values also steadily increased as the scale increased (Fig. 3.2). This finding could be due to differences in crop management between smaller and larger scaled asparagus farms. In chapter two, I found that both deciduous leaves and hollow asparagus stalks were important overwintering shelters for asparagus beetles. Larger conventional farms are typically more carefully managed with insecticide application and residue removal in comparison to smaller farms. Thus, crop management practices, particularly insecticide application could be contributing to the relationship between the proportion of asparagus and beetles. While the effect of insecticide application on beetle abundance between spatial scales was not considered in this study, further investigation into the how different sized fields and their management practices impact asparagus beetle abundance would be useful.

In Cass County, asparagus beetle abundance increased with the proportion of deciduous forest at all scales. The strength of the relationship between the proportion of deciduous forest and beetle abundance steadily declined, with a steep drop at 2000m (Fig. 3.2). These results demonstrate the possible importance of deciduous forest on asparagus beetle abundance, especially in the field's vicinity. These findings could also be informative in better understanding the dispersal abilities of asparagus beetles. Because there is a positive relationship between proportion of deciduous forest and asparagus beetle abundance, the steady decline in z-values with increasing scale demonstrates that perhaps beetles are unable to disperse at larger distances. Conversely, in Oceana county, no effect was observed between total asparagus beetle abundance and the proportion of semi-natural habitat (deciduous forest, evergreen forest, grassland/pasture). A possible explanation could be the variation between landscape cover at a larger scale. For instance, Cass county is dominated with crop habitat while Oceana county is more dominantly covered with semi-natural habitat. Although the influence of landscape variables over 2000m were not considered in my study, they could be playing a role in the variation between beetle response between locations.

To better understand the cumulative effect of landscape variables on total asparagus beetle abundance within both counties, I analyzed beetle abundance and landscape data from both counties (Fig. 3.5). Considering my first hypothesis, landscapes with higher proportions of semi-natural habitat did support a higher abundance of asparagus beetles. These results contradict the findings of previous studies that found increasing semi-natural habitat led to declines in pest abundance (Bianchi et al. 2006, Chaplin-Kramer et al. 2011). This could be due to both bottom-up and top-down factors occurring within the landscape. Firstly, it should be considered that natural enemy populations are not very prevalent in the asparagus agroecosystems used in this study. Previous studies have found that although natural enemies are present, predation within asparagus agroecosystems in Michigan is often low (Ingrao et al. 2017). More likely, instead of supporting natural enemies of asparagus beetles, the semi-natural habitats could be primarily supporting asparagus beetles. As found in Chapter 2, asparagus beetles do sometimes utilize semi-natural habitat as overwintering habitat. It was also found that asparagus beetles survive at higher rates when using deciduous leaves as overwintering shelter compared to other common substrates. Because deciduous leaves can only originate from surrounding semi-natural habitat and increase overwintering beetle survival, these habitats could be more important for the success of asparagus beetle populations. This finding coincides with the 'landscape complementation' hypothesis which suggests that some organisms are dependent on resources from different types of habitat and have higher success when these habitats are in closer proximity to each other (Dunning et al. 1992). Because the strength of the relationship between beetle abundance and deciduous trees was strongest at lower scales (Fig. 3.2, Fig. 3.3B, Table S3.2), the proximity of deciduous trees to asparagus beetle populations seems to be crucial. So perhaps the net impact of the resources being provided to arthropods by semi-natural habitat is stronger for pest populations than natural enemies, as previously suggested (Tscharntke et al. 2016). Other semi-natural habitats investigated in this study, such as the proportion of evergreen forest and grassland/pasture demonstrated relationship with asparagus beetle populations as well, although they did not show as strong of relationships (Fig. 3.2, Table S3.2). Overall, when counties were combined, a greater proportion of semi-natural habitat in a landscape led to a higher abundance of asparagus beetles.

Regarding my second hypothesis, I found that for higher spatial scales (SHDI: 300-2000m, Edge Density: 400-2000m) less diverse landscapes, with lower edge density supported higher abundances of asparagus beetles. Based on the Shannon's Diversity Index, beetle abundance was lower in more diverse, heterogeneous landscapes. This finding coincides with previous studies looking at other pest species responses to landscape diversity (Villa et al. 2020, Clemente-Orta et al. 2020, Dominik et al. 2018). A possible explanation for this finding could be that with higher landscape diversity there is often less crop habitat for insect pests to utilize. Another explanation could be due to the increased occurrence of natural enemies typically found in more diverse landscapes (Gardiner et al. 2009). However, previous literature has suggested that landscape diversity often does not have a large impact on pest suppression by natural enemies (Rusch et al. 2016, Landis 2017, Karp et al. 2018). Martin et al. 2016 found that the influence of landscape composition varied widely between taxa and was mainly driven by the diversity of land cover types surrounding the field. Consequently, further investigation into the influence of landscape diversity on different pest taxa is necessary. While I originally hypothesized that landscapes with higher edge density would support higher beetle populations, I actually found that there was a negative relationship between edge density and beetle abundance at higher spatial scales. Previous research has found that arthropods can spill over between crop and non-crop habitats (Rand et al. 2006, Tscharntke et al. 2012, Blitzer et al. 2012). When edge density is high, there is more potential for spillover between landscapes by arthropods. Gallé et al. 2020 found that smaller farms with higher edge density majorly influences functional traits and ecosystem services like biological control throughout agricultural landscapes. In this study, I found that there was a positive relationship between edge density and total beetle abundance at lower scales- perhaps asparagus beetles are only able to spill over between habitats at lower spatial scales due to low dispersal ability. Higher edge density throughout landscapes has been found to positively impact natural enemy populations (Martin et al. 2019). Natural enemies that overwinter within crop fields have been found to be more abundant when the edge density was low throughout a landscape (Haan et al. 2020). This may be the reason for seeing a negative relationship between beetle abundance at edge density at larger scales. Overall, these results demonstrate that both landscape composition and configuration vary in importance between spatial scales in relation to asparagus beetle abundance.

Conclusions

By understanding how pest populations are influenced by surrounding landscapes, agricultural systems can be redesigned to suppress pests with less insecticide use and more sustainable practices. While the effect of the surrounding landscape varied between counties, when data was combined, I found decrease of asparagus beetle abundance was correlated with landscape configuration, particularly edge density and diversity, at varying scales, both small and large. While previous studies have found that increasing semi-natural habitat can suppress pests, these results found that increasing the proportion of semi-natural habitat (deciduous forest, evergreen forest, grassland) led to higher asparagus beetle abundance. In particular, the proportion of deciduous forest seems to be crucial for the success of asparagus beetle populations. Based on these inconsistent findings on the effect of semi-natural habitat on pest populations, it is important for future studies to investigate traits specific to pest species such as dispersal ability and habitat breadth. Better understanding how landscapes affect different pest species could allow researchers and farmers to more effectively predict and manage pest populations based on these species-specific traits.

APPENDIX

Table S3.1 Summary of the final generalized linear models (with negative binomial error distribution) testing for effects of landscape configuration at a given spatial extent and the summary statistics (estimate values, z-values, p-values, AIC).

Explanatory variable	Spatial extent (m)	Value ± SE	z-value	*p*	AIC
Edge density	100	0.09±0.024	3.926	**<0.001**	13864.33
	200	0.03±0.024	1.446	**0.001**	13876.43
	300	0.01±0.023	0.467	0.64	13878.05
	400	-0.04±0.023	-1.837	0.066	13874.57
	500	-0.07±0.023	-3.066	**0.002**	13867.24
	750	-0.09±0.023	-3.976	**<0.001**	13859.65
	1000	-0.08±0.023	-3.297	**<0.001**	13865.59
	1250	-0.06±0.023	-2.461	**0.014**	13871.54
	1500	-0.07±0.023	-3.015	**0.003**	13868.32
	2000	-0.08±0.023	-3.214	**0.001**	13867.65
SHDI	100	0.15±0.023	6.337	**<0.001**	13841.71
	200	0.02±0.023	0.956	0.339	13877.39
	300	-0.03±0.023	-1.333	0.183	13876.41
	400	-0.04±0.023	-1.683	0.095	13875.17
	500	-0.06±0.023	-2.709	**0.007**	13869.65
	750	-0.05±0.023	-2.295	**0.022**	13872.14
	1000	-0.03±0.023	-1.316	0.188	13876.35
	1250	-0.04±0.023	-1.824	0.068	13874.59
	1500	-0.07±0.023	-2.832	**0.005**	13869.40
	2000	-0.09±0.023	-4.009	**<0.001**	13861.87

*P-values >0.05 are bolded

Table S3.2 Summary of the final generalized linear models (with negative binomial error distribution) testing for effects of landscape composition on total beetle abundance per site at a given spatial extent and the summary statistics (estimate values, z-values, p-values, AIC).

Explanatory variable	Spatial extent (m)	Value ± SE	z-value	*p*	AIC
% Deciduous Forest	100	0.21±0.023	9.195	**<0.001**	13794.06
	200	0.19±0.023	8.303	**<0.001**	13806.18
	300	0.18±0.023	7.891	**<0.001**	13811.46
	400	0.18±0.023	7.716	**<0.001**	13813.57
	500	0.19±0.023	8.104	**<0.001**	13807.90
	750	0.18±0.023	7.648	**<0.001**	13814.66
	1000	0.17±0.023	7.217	**<0.001**	13822.19
	1250	0.17±0.023	7.527	**<0.001**	13822.00
	1500	0.16±0.023	7.037	**<0.001**	13834.02
	2000	0.09±0.023	3.946	**<0.001**	13864.15
% Asparagus	100	-0.14±0.025	-5.741	**<0.001**	13850.56
	200	-0.12±0.024	-5.019	**<0.001**	13857.10
	300	-0.14±0.025	-5.71	**<0.001**	13850.26
	400	-0.16±0.025	-6.363	**<0.001**	13842.42
	500	-0.18±0.025	-7.419	**<0.001**	13828.25
	750	-0.19±0.025	-7.712	**<0.001**	13824.35
	1000	-0.2±0.025	-7.884	**<0.001**	13822.36
	1250	-0.22±0.026	-8.637	**<0.001**	13808.50
	1500	-0.22±0.026	-8.406	**<0.001**	13809.42
	2000	-0.23±0.026	-9.018	**<0.001**	13799.61
% Evergreen	100	0.08±0.023	3.26	**<0.001**	13865.97
	200	0.07±0.023	3.172	**<0.001**	13868.43
	300	0.12±0.023	5.056	**<0.001**	13855.66
	400	0.11±0.023	4.81	**<0.001**	13857.57
	500	0.08±0.023	3.277	**<0.001**	13868.19
	750	0.06±0.023	2.425	**0.015**	13872.68
	1000	0.06±0.023	2.784	**0.0054**	13871.02
	1250	0.06±0.023	2.739	**0.006**	13871.10
	1500	0.07±0.023	2.838	**0.005**	13870.57
	2000	0.07±0.023	2.923	**0.003**	13870.11
% Grassland/Pasture	100	0.05±0.023	2.312	**0.021**	13872.99
	200	0.05±0.023	3.172	**0.002**	13874.28
	300	0.06±0.023	2.421	**0.015**	13872.43
	400	0.06±0.023	2.508	**0.012**	13872.09
	500	0.04±0.023	1.881	0.06	13874.69
	750	0.03±0.023	1.441	0.15	13876.13
	1000	0.06±0.023	2.71	**0.006**	13871.18
	1250	0.07±0.023	3.07	**0.002**	13869.36
	1500	0.09±0.023	3.798	**<0.001**	13864.95
	2000	0.1±0.023	4.427	**<0.001**	13860.59

*P-values >0.05 are bolded

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CHAPTER 4:

Conclusions and future directions

Throughout my thesis, I have investigated how both local habitat and landscape effects are influencing the overwintering biology and overall population dynamics of the common asparagus beetle (*Crioceris asparagi* Coleoptera; Chrysomelidae). Few studies have been conducted on this specialist key pest of *Asparagus officinalis,* yet asparagus beetles have caused significant economic damage to the commercial asparagus industry. With Michigan being the leading producer of asparagus in the United States, most commercial growers have become dependent on managing this pest by conventional insecticide application. To help create more sustainable, economically and environmentally, management methods, I investigated which habitats and resources are promoting asparagus beetle overwintering survival and seasonal abundance both on a local and landscape scale.

In Chapter 2, my research focused on assessing how local factors throughout the asparagus agroecosystem are impacting overwintering asparagus beetles. Few previous studies have focused on the overwintering biology of insect pests, and no prior research has been conducted looking at the overwintering of asparagus beetles (Sutter et al. 2018, Leather 1993). While no formal studies have been conducted, vegetable extension agents and asparagus growers had noticed that asparagus beetles seemed to be utilizing overwintering shelter both inside and outside of the field, such as hollow asparagus stalks and tree bark (John Bakker, personal communications). Because these substrates can be found throughout different habitats within asparagus agroecosystems, I decided to further explore where asparagus beetle populations were primarily overwintering. This research demonstrated that asparagus beetles are primarily overwintering within asparagus fields, although some of the population is utilizing field margins and woodlots as overwintering habitat as well. I was also interested in investigating which overwintering substrates (e.g., leaves, bark, hollow asparagus stalks) promoted asparagus beetle survival. My findings demonstrated that asparagus beetles survive at the highest rates within deciduous leaves, with hollow asparagus stalks also being an important overwintering shelter. While hollow asparagus stalks are a product from the asparagus field itself, the deciduous leaves that seem crucial to asparagus beetle overwintering success originate from the surrounding habitat. Based on these compelling results, I was interested in learning more about how the composition of the surrounding tree community impacted asparagus beetle populations. Because the overwintering success of asparagus beetles seemed dependent on deciduous leaves, I expected to see a positive relationship between deciduous and live trees, and the abundance of asparagus beetles. However, I did not find any relationship between the number of deciduous or live trees and the abundance of asparagus beetles. I did find a negative trend between dead trees and the abundance of asparagus beetles, which does imply that there could be a relationship, but further exploration is necessary. Factors such as variation in vegetation health between years could have played a role in this lack of findings. The results of this analysis suggest that asparagus beetles rely on resources both inside and outside the crop field for their overwintering success, but growers should focus their efforts on management within the field.

In Chapter 3, my research focused on better understanding how landscape composition and configuration are influencing asparagus beetle populations throughout various spatial scales. While no previous studies focusing on the landscape effects of asparagus beetles have been conducted, there have been prior studies focused on how landscape composition impacts arthropod populations, beneficial and pest, within agroecosystems (Zhang et al. 2020, Villa et al. 2020, Rusch et al. 2013). Most of these studies have focused on how natural enemies are impacted by the landscape composition, and how that indirectly impacts pest populations. However, a recent meta-analysis of pest-focused studies found that there were inconsistent responses to the surrounding landscape composition by pest populations (Karp et al. 2018). Another recent analysis found that pest species with varying pest traits responded differently to the composition of the surrounding landscape (Tamburini et al. 2020). Consequently, I decided to explore how different parameters of landscape composition were impacting asparagus beetle abundance throughout the growing season. While the influence of the surrounding landscape on total beetle abundance varied between counties, my combined findings demonstrated a positive relationship between asparagus beetle abundance and the proportion of semi-natural habitat across all examined spatial scales. In particular, the proportion of deciduous trees seemed to influence asparagus beetle abundance the most at lower scales, which could be an indication of the dispersal abilities of asparagus beetles. The proportion of asparagus showed a negative effect on asparagus beetle abundance, with increasing importance as the scale increased. Because growers manage large farms more intensely, these findings could be due to differences in crop management between smaller and larger scaled farms. Consequently, the landscape composition of arthropods has been well studied, but the impact of landscape configuration is only recently becoming more prevalent. While landscape composition looks at the amount of land cover in a landscape, landscape configuration looks at the spatial arrangement of these land covers (Fahrig et al. 2011). Particularly, I was interested in exploring how the diversity and evenness, and edge density of the surrounding landscape impacted asparagus beetle abundance. My findings indicated that both landscape diversity and edge density had a negative relationship with asparagus beetle abundance at higher spatial scales. These findings suggest that having smaller farms, and more diverse surrounding landscapes promote pest suppression either from bottom-up or top-down processes. This research was able to demonstrate the importance of both landscape composition and configuration on an insect pest, and how agricultural landscapes could potentially be redesigned to promote pest suppression within crop fields.

Ultimately, my thesis helped demonstrate how both local and landscape effects are impacting the populations of both overwintering and active asparagus beetles. According to my findings, asparagus beetles are primarily overwintering within asparagus fields, with improved overwintering success when utilizing deciduous leaves as overwintering shelter. Although I did not find a direct relationship between the number of deciduous or live trees and asparagus beetle abundance, my findings suggest that the composition of the surrounding tree community could be influencing asparagus beetle population dynamics. Because the number of dead trees demonstrated a negative effect on asparagus beetle abundance, the influence of surrounding vegetation health should be further investigated. Landscape composition and configuration were also shown to influence asparagus beetle abundance. Landscapes with higher proportions of semi-natural habitat (deciduous forest, evergreen forest, grassland) had higher populations of asparagus beetles. Put together, my findings suggest that surrounding habitat and landscapes are supporting overwintering asparagus beetle populations, particularly deciduous trees found within semi-natural habitat. The diversity and edge density of land covers throughout the landscape also influenced asparagus beetle abundance, demonstrating the importance of the size and variety of land covers surrounding asparagus fields on pest populations. The findings of this thesis have helped demonstrate that the influence of the surrounding habitat and landscape on an insect pest is species-dependent and can dramatically vary. Future research should investigate how the composition and configuration of agricultural landscapes, locally and regionally, are influencing different pest traits (e.g., dispersal, habitat breadth, exotic status) that are present within pest communities, and how to use this information to better predict pest population dynamics. By identifying species-specific traits of key insect pests, more targeted management strategies can be implemented into asparagus production and other cropping systems.

APPENDIX

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: 2021-01

Author and Title of thesis:
Author: Jennifer Zavalnitskaya
Title: Habitat Management and Landscape Influence *Crioceris asparagi* (Coleoptera: Chrysomelidae) Overwintering Biology and Population Dynamics

Museum(s) where deposited:
Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Specimens:

Table S. 1. Voucher specimens deposited at the Albert J. Cook Arthropod Research Collection (Michigan State University).

Family	Genus-Species	Life Stage	Quantity	Preservation
Chrysomelidae	*Crioceris asparagi*	Adult	10	pinned

LITERATURE CITED

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