THE SPATIAL AND TEMPORAL DISTRIBUTION OF ARTHROPODS IN MICHIGAN CELERY AGROECOSYSTEMS

By

Jeremy J. Jubenville

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Entomology - Master of Science

2015

ABSTRACT

THE SPATIAL AND TEMPORAL DISTRIBUTION OF ARTHROPODS IN MICHIGAN CELERY AGROECOSYSTEMS

By

Jeremy J. Jubenville

Understanding the source of insects within an agricultural production system is essential to selecting the most suitable management practices. In this thesis, I examine the spatial patterns of arthropods in Michigan commercial celery systems and evaluate whether field margins are sources of insects therein. Insect abundance was measured at different distances within six different celery fields located in southwest Michigan during 2013 and 2014. Most herbivores were evenly distributed throughout the field, although minor edge effects were detected when overall abundance was low. Herbivore abundance in margins, relative to the field, varied across groups; tarnished plant bugs and leafhoppers are key pests that may be using margins for habitat. Most predators were evenly distributed across the field. Syrphid flies were more abundant in margins, suggesting greater association with these areas than other groups. Parasitoid abundance was also consistently margin-centric across groups during both seasons. In 2014, I performed a mark-capture experiment in which three field margins were sprayed with a protein marker. Arthropods were subsequently captured and tested for the presence of the protein. Most groups had at least one individual testing positive for the presence of the marker, but the majority of specimens in every group tested negative. Variation in mark percentage, as well as the spatial distribution of marks, showed that some groups, such as tarnished plant bugs and syrphid flies, utilize the margins more than others. Any systematic change in the way growers manage their margins would likely affect these groups to a greater degree than the other groups in the study.

ACKNOWLEDGEMENTS

I would like to thank Zsofia Szendrei for providing the opportunities and conditions that facilitated my academic and professional development. I could not have asked for a better advisor. I also would like to thank the other members of my graduate committee, Doug Landis and Phil Robertson, for their wisdom and support; the most influential guidance always came in the form of a question. I greatly appreciate the southwest Michigan celery farmers who let me do this work in their fields: Ron Eding, Jake Willbrandt, Mark Cnossen, and Bruce & Eric Schreur. I am truly indebted to Jen Lau and Kay Gross for their hospitality and support during my extended visit to Kellogg Biological Station. There is no way that I would have been able to complete this project without the help of Andy Galimberti, Alec Ashburn, Angie Lane, Jessica Kansman, and Gabriel King. I am thankful for the help of Mark Hammond and Cindy Mills, lab managers extraordinaire. My research and graduate degree were supported by Project GREEEN, the Rhodes (Gene) Thompson Memorial Fellowship, a Michigan Vegetable Council scholarship, and two G.H Lauff scholarships from KBS. My summer undergraduate assistant, Gabriel King, was supported by the KBS URA program in conjunction the MSU College of Agriculture and Natural Resources. Finally, I would like to express my deepest love and appreciation for my wife, Megan, for her support during the whole process. This would not have happened without her encouragement.

I dedicate this thesis to my grandparents, John T. and W. Lou Bush, who showed me the value of hard work, persistence, and resourcefulness. I wish they could see me now.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1:

Spatial ecology of arthropods and celery production in southwest Michigan

Introduction

Celery (*Apium graveolens*) is a biennial plant in the Apiaceae selected for its large succulent petioles. Although there is historical record of celery usage around the 4th century BCE as a medicinal herb, cultivation as an edible vegetable began in Europe around the 17th century (Levine 2013). It was first established as a commercial crop in the United States during the late 19th century in Kalamazoo, MI (Berger *et al*. 1988, Levine 2013). Michigan currently accounts for 5.5% of total U.S celery production with 98.5 million pounds harvested from 1700 acres and a market value of just under $19 million (USDA NASS, 2015). Although most of the production in Michigan occurs in the southwest region of the state, there is notable acreage in the west central and eastern counties as well.

Most, if not all, commercial celery production in Michigan occurs on muck soils (histosols) (Zandstra *et al*. 1986, Wong *et al*. 2010). In temperate latitudes, cultivated muck soils are usually remnant geographic water features that have either dried up due to natural processes or have been intentionally drained for cultivation (Brady & Weil 2007, Lindbo & Kozlowski 2005). By their nature, muck soils are often found in low-lying areas where the water table has historically been near or above the surface. Fields in these systems are susceptible to flooding, which can damage a crop under prolonged circumstances. Growers manage excess water with a combination of drainage tiling, water pumps, ditches, and dikes (J. Jubenville pers. obs., Brady & Weil 2007, Lindbo & Kozlowski 2005). Consequently, celery farms tend to have long, narrow fields (e.g. 400-800m x 50m) that are bordered on two or three sides by drainage ditches.

The organic matter content of muck is high when compared to the more common mineral soils, resulting in a fine-textured, nutrient-rich growing medium (Brady & Weil 2007, Lindbo & Kozlowski 2005). Muck systems are innately productive due to this high percentage of humus in the soil and a consistent water supply. When dry and bare, however, these soils are so light that they are highly susceptible to wind erosion. In the spring, some growers will cover freshly transplanted fields with a woven material to mitigate soil loss and protect the young plants from chafing by blowing soil (Zandstra *et al.* 1986, E. Schreur, pers. comm., J. Jubenville, pers. obs.). Retaining these soils is a persistent challenge; consistent cultivation results in annual losses from erosion and oxidation of organic matter (Lucas 1982, Brady & Weil 2007, Lindbo & Kozlowski 2005). Even with these drawbacks, the characteristics of muck soil make it an excellent growing medium for celery and many other vegetables (Zandstra *et al.* 1986, Brady & Weil 2007, Lindbo & Kozlowski 2005).

There are two main types of cultivated celery, 'Pascal', which has green stalks (petioles), and 'Golden Heart' (a.k.a. 'Kalamazoo') which "self-blanches" and has white stalks (Zandstra *et al*. 1986, Levine 2013). Three cultivars of Pascal celery that are currently popular with Michigan growers are 'Green Bay' for favorable fresh market characteristics, 'Sabroso' for processing, and 'Dutchess', which is used as a dual-purpose cultivar. Michigan growers start celery from seed inside greenhouses in mid-February where they are nurtured for approximately eight weeks. Seedlings are then transplanted into the field around mid-April at a density of ~40,000 plants/acre.

Field preparation consists largely of amendments and cultivation, although drainage issues are occasionally addressed. Cover crops, if any, will have been turned under and a pre-emergent herbicide is sometimes applied (Hausbeck 2011, Zandstra 2012). Many growers will

use either a Brassica (oilseed radish) or Sorghum-sudan grass as a cover crop specifically for their anti-microbial properties (J. Eding pers. comm., Wong *et al*. 2010). Cold temperatures can cause premature bolting in celery plants, so early-Spring transplants are sometimes protected by row or field covers (Zandstra *et al*. 1986). Celery remains in the field 80-95 days depending on the cultivar, growing conditions, and harvest schedule. Mechanical harvesting is a frequent option, although some growers employ workers to harvest by hand when the produce is designated for fresh market.

Weeds in celery

The characteristics of muck soils that make them desirable for growing vegetables are also favorable to weed growth. The list of weeds common among these systems is long, and several of them in our region have developed resistance to herbicide (R Eding pers. comm. M. Cnossen pers. comm., J. Willbrandt pers. comm., Zandstra 2012). Some of the most common weeds are pigweed (*Amaranthus spp*.), giant ragweed (*Ambrosia trifida*), lamb's quarter (*Chenopodium album*), common ragweed (*Ambrosia artemisiifolia*) velvetleaf (*Abutilon theophrasti*), smartweed (*Polygonum* spp.), purslane (*Portulaca oleracea*), and yellow nutsedge (*Cyperus esculentus*) (J. Jubenville pers. obs., Hausbeck, 2011). Growers are proficient at keeping their fields relatively free of weeds. Nevertheless, these species occur persistently along the numerous margins and ditches that occur in these systems. Plant species that are common and abundant within these marginal areas include, giant ragweed, velvetleaf, pigweed, wild carrot (*Daucus carota*), poison hemlock (*Conium maculatum*), smartweed, field bindweed (*Convolvulus arvensis*), common nettle (*Urtica dioica*), common milkweed (*Asclepias syriaca*), yellow nutsedge, and assorted grasses. Margin weed management consists of cultivation,

mowing, or post-emergent herbicide (Hausbeck 2011, Zandstra 1986). Mowing may be the most common method employed and occurs in any given field approximately once per month.

Pathogens of celery

In the suite of plant pathogens that attack celery, some of the most important are foliar blights caused by the fungi *Septoria apiicola* and *Cercospora apii*, a bacterial blight caused by *Pseudomonas syringae* pv. *apii*, Fusarium yellows caused by the fungus *Fusarium oxysporum*, and the Aster yellows phytoplasma (Lacy *et al*. 1996, Hausbeck 2011). *Colletotrichum acutatum* is a fungus recently indentified from samples taken from commercial celery fields in Michigan (Rodríguez-Salamanca *et al*. 2012). Although *Colletotrichum* spp. have been known to cause anthracnose in a variety of other fruit and vegetable commodities, this disease was previously unconfirmed in Michigan celery (Peres *et al.* 2005, Dillard 1992, Rodríguez-Salamanca *et al*. 2012). Disease caused by the *Septoria* fungus occurs every year and is the most common pathogen problem in Michigan commercial celery fields (Hausbeck 2011).

Insect pests in celery

Some of the major insect pests of celery are aphids (*Aphis spiraecola, Aphis helianthi, Myzus persicae*, etc.), the tarnished plant bug (*Lygus lineolaris*), the aster leafhopper (*Macrosteles quadrilineatus*), and the variegated cutworm (*Peridroma saucia*). Minor pests include the two-spotted spider mite (*Tetranychus urticae*), the carrot weevil (*Listronotus oregonensis*), and thrips (Thysanopetera: Thripidae). The celery leaftier (*Udea rubigalis*), along with slugs, leafminers (Diptera: Agromyzidae), and loopers (Lepidoptera: Noctuidae) can cause great damage in large numbers, but are best described as sporadic pests in Michigan celery fields.

Aphids. Aphids are small soft-bodied insects that insert their piercing and sucking mouthparts into plant phloem tissue to obtain sugars and nutrients. The general aphid life cycle in the northern United States is as follows (summarized from Dixon 1977, 1985): they overwinter as eggs on a primary host plant and hatch as wingless females in the spring. These females produce genetically identical offspring by viviparous parthenogenesis, with several generations continuing in this manner. As the weather warms, aphid populations will start to produce winged females that disperse to other plant hosts and once again produce wingless offspring. As fall and winter approach, winged females fly back to their primary hosts to produce both male and female offspring for mating. Mated females will lay eggs on the primary plant host to pass the winter and the process repeats itself the following spring.

The spirea aphid, *Aphis spiraecola* (Hemiptera:Aphididae), has been identified (D. Lagos and D. Voegtlin, pers. comm.) as the species responsible for recent infestations in southwest Michigan celery fields. It is a small (1.2-2.2mm) yellow-green aphid with black cauda and black siphunculi (Fig. 1.1). The thorax in the alatae is dark brown or black, while that of the aptarae are

Figure 1.1. Spirea aphids feeding on a celery leaf. (Photo: Z. Szendrei)

the same color as the abdomen. *Aphis spiraecola* originated in East Asia, was first recorded in the United States in 1907, and is now distributed throughout the world (Blackman and Eastop 2007). It is a highly polyphagous species with known hosts in twenty plant families, including the Apiaceae, and is one of the most important pests of citrus crops in the United States (Blackman and Eastop 2007). *Aphis spiraecola* can be difficult to identify in the field due to variable (Lowery *et al.* 2002) but generally similar morphology to many other aphid species (e.g. *A. citricola*, *A. pomi*, *A. eugeniae*) (Halbert and Voegtlin 1992, Footit *et al.* 2009, Blackman & Eastop 2007). In celery, the spirea aphids can easily be confused with the cotton-melon aphid (*A. gossypii*) and, to a lesser extent, the green peach aphid (*Myzus persicae*) and the sunflower aphid (*A. helianthi*).

In warmer climates, *A. spiraecola* populations are usually permanently parthenogenetic (Blackman and Eastop 2007). Populations in the northern U.S. and East Asia, however, are cyclically parthenogenetic and are known for using *Spirea* spp. as primary hosts for overwintering. Nevertheless, there are specific populations in Japan that use *Citrus* spp. as a primary host and research in Washington apple crops (Lowery *et al.* 2002) suggest that there are some populations that overwinter on apple trees (*Malus* spp.). Thus, while *Spirea* spp. can be considered the most likely primary host for any given population, it is not guaranteed to be the only primary host.

Aphid infestations can produce curling and distortion in leaves, fungal growth on excreted honeydew, and excessive amounts of exuvia, which together can render a vegetable plant unsuitable for fresh market. In celery, *A. spiraecola* tend to aggregate on young tissue near the top of the petioles; infestations can be obvious to the eye. Although disease transmission is a concern with phloem-feeders, incidence seems to be lower with *A. spiraecola* until populations

grow large (Blackman and Eastop 2007). Far more concerning, however, is the development of pesticide resistance in Spirea aphids that have been reported in other crops (Hogmire *et al.* 1992, Smirle *et al*. 2010, Blackman & Eastop 2007) and is likely causing problems for Michigan celery growers (Z. Szendrei, pers. comm.).

Aster leafhopper. The aster leafhopper, *Macrosteles quadrilineatus* Forbes (Hempitera: Cicadellidae), is a small (~3mm) yellowish-green leafhopper with six black spots across the head and smoke-colored wings. It is arguably the most concerning of insect pests to celery growers due to its ability to vector the Aster Yellows phytoplasma (AYp), a cell wall-less bacteria-like organism that causes the Aster Yellows disease in vascular plants (Meade and Peterson 1964, Beanland *et al*. 2005, Christensen *et al*. 2005, Frost *et al*. 2011). *Macrosteles quadrilineatus* is distributed widely across the continental U.S. (both east and west of the Rocky Mountains) and is known to migrate thousands of miles every spring from southern locations to the northern states (Westdal *et al*. 1961, Meade and Peterson 1964, Hoy *et al*. 1992). The aster leafhopper can also overwinter as eggs on foliage as far north as Manitoba and Quebec (Westdal *et al*. 1961). Thus, locally observed populations in the Midwest are likely comprised of both migrant and overwintered individuals. The host range for the aster leafhopper is broad, having been recorded on over 300 plants and many commercial vegetable crops, including celery (Wallis 1962, Frost *et al*. 2011). Likewise, the AYp has been found in over 300 plant species and causes physiological distortions such as twisting, stunting, adventitious roots, and chlorosis in the infected host (Christensen *et al*. 2005, Frost *et al*. 2011). In commercial vegetable production, the quick spread of this disease can render an entire crop unmarketable (Hoy *et al*. 1992).

Tarnished plant bug. The tarnished plant bug, *Lygus lineolaris* (Hemiptera: Miridae), is an herbivore with a geographical range as broad as its dietary niche. Its distribution encompasses the United States as well as southern Canada, and has been found as far north as the Yukon and Alaska (Kelton 1975, Young 1986, Capinera 2001). The tarnished plant bug is a true generalist, having been observed to feed on over 300 plant species (Young 1986), although growth, development, and fecundity has been shown to vary with hosts. Previous research indicates a strong association with early secondary successional communities and weedy margins (Snodgrass *et al.* 1984, Young 1986, Capinera 2001, Snodgrass *et al.* 2005, Outward *et al.* 2008), giving it a reputation as a "border species".

Tarnished plant bugs overwinter as adults and emerge early in the spring to feed on the local flora. Oviposition occurs shortly thereafter with eggs hatching in 1-2 weeks depending on the temperature (Ridgeway and Gyrisco 1960). There are five instars that, with warm weather, can proceed to the adult stage in approximately twenty days (Ridgeway and Gyrisco 1960). Longevity in adults ranges from 40-60 days for females and 30-40 days for males (Capinera 2001). In southwest Michigan, there are probably three generations per year.

Lygus bugs, including the tarnished plant bug, have an extensive suite of natural enemies. The most important parasitoids are reported to be the mymarid egg parisitoid *Anaphes iole* (Hymenoptera: Mymaridae) and several nymphal parasitoids from the Braconidae: *Leiophron uniformes*, *Peristenus palipes*, *P. relictus*, and *P. pseudopallipes* (Clancy and Pierce 1966, Scales 1973, Graham *et al*. 1986, Norton *et al*. 1992, Braun *et al*. 2001, Seymour *et al*. 2005, Pickett *et al*. 2009). Documented predators include *Nabis* spp., *Orius* spp., *Geocoris* spp., *Zelus* spp., the spined soldier bug (*Podisus maculiventris*), spiders, ants, and lady beetles (Leigh and Gonzalez 1976, Whalon and Parker 1978, Hagler 2011).

Damage to plants from tarnished plant bugs varies with the species. In general, they seem to prefer new (meristematic) tissue and reproductive structures (Boersma and Luckman 1970, Khattat and Stewart 1975, Schafers 1980, Grafius and Morrow 1982, Fleischer and Gaylor 1987, Attanazov *et al.* 2002, Foshee *et al*. 2008). Because celery in Michigan is not grown for seed, lygus bugs will instead feed on the new tissue in the heart of the celery. Feeding damage to the young tissue causes discoloration and leaf distortion, often rendering the plant unmarketable (Stewart and Khoury 1978, Boivin *et al.* 1991).

Spatial ecology of arthropods

One of the defining characteristics of agricultural systems is consistent periodic disturbance (Landis and Marino 1999, Landis *et al.* 2000). Ecological disturbance can be defined as an event that causes a change in the spatial patterns of organisms in an ecological system (Wissinger 1997, Debinski and Holt 2000, Tscharntke *et al*. 2005b, Schowalter 2012). These changes are often due to mortality and, in natural habitats, can be caused by events that range in scale from small fires to regional droughts and natural disasters. Disturbance in an agricultural system often comes in the form of plant or pest management practices such as plowing, harvesting, pesticide application, and mowing. In celery fields, most disturbance to the insect community comes from frequent pesticide applications. These disturbances are often intense and almost always result in a mass local extinction of whole groups of organisms, including pestiferous and beneficial insects.

The purpose of this study is to explain the patterns of distribution and abundance of insect groups within celery fields. Explanation requires an analysis based on multiple spatial scales (Tscharntke *et al.* 2005b). To a certain extent, what we find in celery fields and their border habitats is the result of filtering of regional species pools by the local environment and

biotic interactions (competition, predation, mutualism) (Leibold *et al.* 2004,Tscharntke *et al.* 2005a). Biodiversity at any particular location can also be influenced by the surrounding landscape, which functions at a scale in between the locality and the region (Steffan-Dewenter *et al*. 2002, Tscharntke and Brandl 2004, Tscharntke *et al*. 2005). Agricultural landscapes are a mosaic of ecosystems that reflect human land-use patterns, where natural structural and ecosystem heterogeneity is replaced with a collection of simplified monocultural cropping systems (Tscharntke *et al*. 2002, 2005). Natural and semi-natural fragments (hedge rows, field margins, etc.) are interspersed among crop fields, roads, and developed property to create heterogeneity and structural complexity that is much different than the previously existing natural areas (Tscharntke *et al*. 2002, 2005a, 2007). Spatial separation of habitats may require some species to exploit resources from a number of disconnected habitats (Steffan-Dewenter *et al*. 2002, Theis *et al*. 2003, Tscharntke and Brandl 2004). Therefore, understanding local population and community dynamics in a landscape in which habitats of various size and shape are fragmented, poorly-connected, or completely isolated requires analysis at multiple spatial scales.

There are a couple of influential models that have informed our understanding of spatial ecology (Tscharntke and Brandl 2004, Rand and Louda 2006) and are often applied as a conceptual basis for predicting insect diversity in agricultural systems: island biogeography theory (IBT) (MacArthur and Wilson 1967) and metapopulation theory (Levins 1969). IBT predicts lower species richness with decreasing island size and increasing isolation. Although developed to predict biodiversity on ocean islands, it has been applied to predict diversity in terrestrial natural habitats embedded within an anthropogenically-altered matrix (i.e. the terrestrial "ocean") with varying degrees of success (Fahrig and Merriam 1994, Kruess and

Tscharntke 1994, Rozenzweig 1995, Debinski and Holt 2000, Cook *et al.* 2002, Rousch *et al.* 2013). The greatest limitation of IBT in predicting biodiversity in a fragmented landscape is that natural habitats are not usually surrounded by a wholly hostile matrix (e.g. the ocean to an island) and may provide resources for habitat generalists (Janzen 1983, Marino and Landis 1996, Jonsen and Fahrig 1997, Landis *et al*. 2000, Cook *et al.* 2002, Tscharntke *et al.* 2002, 2005b, Tscharntke and Brandl 2004, Rand *et al*. 2006). Species spillover from several types of habitats can result in a greater alpha diversity for individual fragments and greater beta diversity for the landscape than IBT would predict (Tscharntke *et al*. 2002, Leibold *et al.* 2004, Tylianakis *et al.* 2005, 2006).

Metapopulation theory is concerned with extinction and colonization dynamics across a collection of habitats within a given area. It is used to predict the likelihood of a particular species occupying habitat patches within a landscape and can be expressed as a ratio of the number of extinctions across patches to the number of colonizations of previously unoccupied patches over a given period of time. Like IBT, metapopulation theory has its own set of limitations that are, in this case, largely rooted in its general simplicity (Hanski 1998, Tscharntke *et al.* 2005b). Expansions of this theory have overcome some of the limitations by including spatially explicit components and accommodating community interactions and local population dynamics (Hanski 1998). The increase in realism and predictive accuracy, however, is accompanied by substantial complexity (Hanski 1998), the discussion of which is beyond the scope of this thesis. I used metapopulation theory here simply as general framework for understanding: 1) that there are source-sink dynamics and bi-directional movement patterns among insect populations across habitat patches within agricultural landscapes (Shmida and Wilson 1985, Holt 1993, Pulliam 1998, Bianchi *et al.* 2006, Tscharntke *et al.* 2007), and 2)

without immigration, extinction is the only major force acting on local populations (Levins 1969, Hanski 1998).

The combination of IBT and metapopulation theories lead to several predictions that are germane to the subject of insect pests and natural enemies in agricultural mosaics: the effects of dispersal ability on species persistence within a fragmented landscape, niche breadth, and the differential effects of habitat fragmentation across trophic levels. Greater dispersal ability allows for a greater chance to encounter and colonize isolated patches within the landscape (MacArthur and Wilson 1967, Hanski 1998, Fahrig 2003). Species with lower vagility experience a greater risk for regional extinction because emigrants from isolated patches may not be able to locate other suitable patches (Hanski 1998, van Nouhuys and Hanski 2002, Fahrig 2003). Fragmentation is not predicted to be as important as overall habitat loss to generalist species due to their ability to exploit resources from a variety of habitats (Jonsen and Fahrig 1997, Krauss *et al.* 2003). Even with lower dispersal ability, a generalist may only need to travel a short distance to find necessary resources. Specialists, however, are predicted to be at a disadvantage due to a combination of habitat loss, greater isolation of suitable habitats, and dependence on the persistence of another species (Holt *et al.* 1999, 2002, van Nouhuys and Hanski 2002). Should their obligate prey or host aggregate preferentially in agricultural fields, their necessary resource may disappear completely in the event of a pesticide application. Finally, because population densities at higher trophic levels tend to be lower and more variable, the risk for extinction of local populations increases with isolation and habitat reduction (Kruess and Tscharntke 1994, Holt 2002). This effect is predicted to be greater for parasitoids than predators due to their propensity for host specificity (van Nouhuys and Hanski 1999, Holt 2002). Consequently, local

extinction of natural enemy populations may release herbivores from top-down control and increase the likelihood of an outbreak (Kruess and Tscharntke 1994).

Disturbance and recolonization in celery fields

Field sizes and shapes for growing celery in southwest Michigan varies based on the total area of muck soil available at any particular location. Some growers engage in "pocket muck farming" (Bruce Klamer, pers. comm.) by exploiting multiple small pockets of muck soil distributed over the landscape. These small fields are likely the remains of old ponds and are often subject to flooding after strong rains due to the fact that muck occurs naturally in low-lying areas. Installing drainage technology in these small areas is probably not economical and so the growers simply tolerate the occasional flooding. Large areas of muck, on the other hand, benefit from the economy of scale and so growers will often construct and install a network of drainage ditches and tiling to lower the water table across the entire area of muck soil. A common result of this strategy is an aggregation of long narrow fields across the muck area, each bordered on two or three sides by drainage ditches. The actual width of these fields are based on grower equipment, but are often ~50m wide (J. Jubenville, pers. observation, Fig. 1.2A-B). The width of a drainage ditch varies, but is typically 2-3m wide. Some growers cultivate the soil as close to the slope of the ditch as possible to maximize growing area and reduce weed pressure, whereas some leave uncultivated space on both sides to create a fairly wide crop-free space between fields. This crop-free space can be 6-7m wide and is usually populated by a mixture of agricultural weeds and regional flora (Figs. 1.3A-B, 1.4A). Growers do not usually allow the plants in these areas to grow significantly and mow or spray herbicide to control them (Fig. 1.3A-B). Mowing occurs, on average, once per month during the season; herbicide application usually happens just before transplanting and can be the only

Figure 1.2. Satellite images of celery fields from two different farms in (A) Allegan County and (B) Van Buren County in southwest Michigan. Arrows indicate some celery fields throughout the landscape in Van Buren County; each of these fields is approximately 50m wide. Note that many fields are long, narrow, and are bordered lengthwise by ditches.

margin management needed for the life of the crop (R. Eding. pers. comm., Zandstra 1986). In addition to this management, growers will often leave cultivated, plant-free soil as a buffer zone between margins and the crop. This buffer zone results in a "hard" visual interface between the lush green crop, the dark muck soil, and the weedy margin-ditch area (1.4A-B). Thus, the

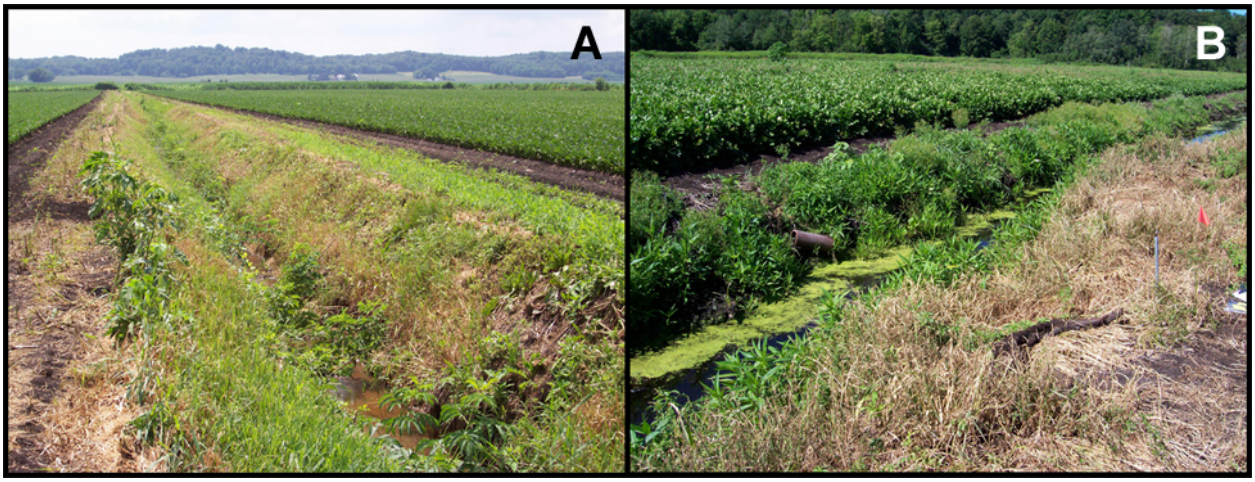

Figure 1.3. Photographs of marginal areas bordering celery fields from two different farms in (A) Van Buren County and (B) Allegan County in southwest Michigan. Margins and ditch banks are managed with mowing (A) or herbicides (B).

arrangement of the celery crop, drainage ditches, and their margins results in smaller fields with a higher edge-to-area ratio than crops grown on upland mineral soils (e.g. corn/soy/wheat, squash, solanaceous fruit).

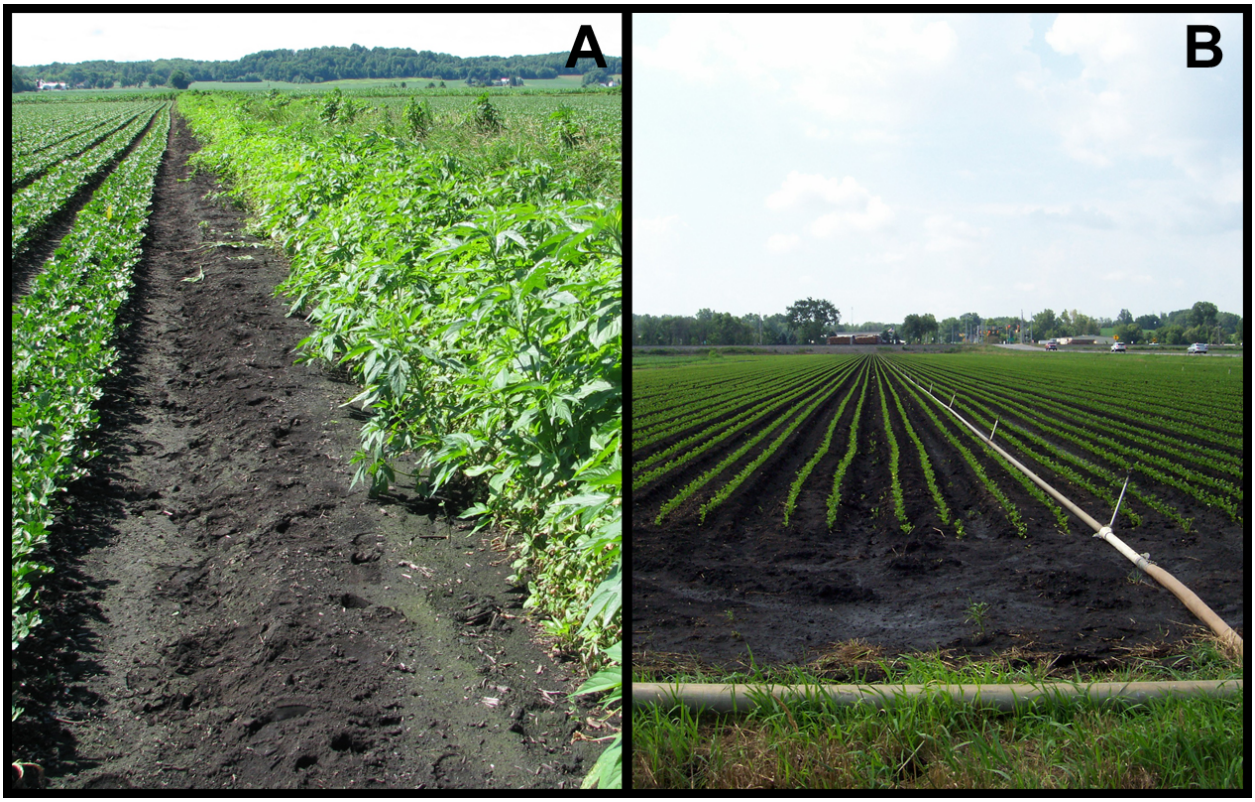

Figure 1.4. Photographs of celery fields from two different farms in (A) Van Buren County and (B) Ottowa County in southwest Michigan. Note the sharp interface between crop, soil, and margin vegetation.

Fungicide application for most growers occurs on a weekly calendar-day basis (E. Schreur & R. Eding pers. comm) and many will add a broad-spectrum insecticide to the spray tank as a matter of economy (R. Eding & M. Cnossen pers. comm., Table 1.1, Table 1.2). This weekly insecticide treatment eliminates virtually all arthropods from celery fields, but insects have often re-colonized these areas by the time of the next application (J. Jubenville, pers. obs.). In general, insect colonists could come from three places: natural areas within the landscape,

semi-natural or less-disturbed areas (e.g. hedgerows, margins, recreational areas), and the aerial plankton species pool (i.e. migrant and wind-borne organisms) (Buntin *et al.* 1990). Understanding the source of insects has important management implications. Margins may be especially important to insects on celery farms. The high number of margins in these systems could provide temporary refuge from pesticides and potentially serve as an immediate source of insects to re-colonize the crop (Landis *et al*. 2000, Lee *et al.* 2001). Furthermore, field margins and other border habitats are the only potential sources within the complete control of the grower.

If we think of a celery field immediately after insecticide application as an uninhabited island, we can use a combination of IBT and metapopulation theory as well as our knowledge of grower management practice to predict both the sources of re-colonizing insects and their distribution patterns within the field. The length of time it takes for an insect colonist to reach these "islands" depends upon its dispersal strength and the relative isolation of the field (MacArthur and Wilson 1967, Levins 1969, Hanski 1998, Schowalter 2012). Margins, the closest potential source of insects within these systems, experience high-levels of disturbance (mowing, herbicide), but not in the same form or frequency as the crop. The period between disturbances may be enough time for incipient insect populations to grow via recruitment as well as immigration. Thus, it is reasonable to consider the possibility of a source-sink relationship between the margins and the crop. In this scenario, the network of margins could serve as sources, refuges, and corridors that help facilitate the persistence and dispersal of insects across the farm (Haddad 1999, 2003, Collinge 2000, Debinski and Holt 2000, Landis *et al*. 2000, Lee *et al.* 2001, Nicholls *et al.* 2001, Van Dyck and Baguette 2005, Conradt and Roper 2006, Holzschuh *et al.* 2009, Delattre *et al.* 2010).

Sources and distribution patterns of any particular group or species in this situation should be strongly correlated to its dispersal ability. We know from previous research that colonization of highly disturbed areas usually occurs at the edges first and proceeds inward (Schowalter 2012). Because these fields are so narrow, however, we can expect to find that high-dispersal species might be able to reach the middle of these fields (~25m) rather easily, showing uniform distribution patterns. Species that are less mobile may take longer to colonize the area, possibly reflected by a pattern of decreasing abundance with increasing distance from the field edge. Given the narrow field profile with a short distance to the middle, a consistent edge-oriented colonization pattern could signify that margins are a source for insects. If any of these insects also happen to be pests, then this knowledge can inform future margin management decisions.

Thesis objectives

The intent of this thesis is to document and analyze the arthropod community in Michigan commercial celery fields. The first objective is to document the spatiotemporal abundance patterns of the arthropod community and determine the most important groups. The second objective is to evaluate the efficacy of current margin management practices and determine if margins are a major source of the insects that we find in the field.

Table 1.1. Table of pesticide mixtures from a southwest Michigan celery farm in 2014. Insecticides, highlighted in red text, were added to every application of fungicide or herbicide.

Grower Mix	Product	Use	Insecticide Class
Mixture #1	Permethrin 3.2	insecticide	**pyrethroid**
	Chloronil	fungicide	
	Nu Cop	fungicide-bactericide	
Mixture #2	Acephate	insecticide	**organophosphate**
	Chloronil	fungicide	
	Nu Cop	fungicide-bactericide	
Mixture #3	Permethrin 3.2	insecticide	**pyrethroid**
	Dimethoate 4EC	insecticide	**organophosphate**
	Chloronil	fungicide	
	Nu Cop	fungicide-bactericide	
Mixture #4	Lannate LV	insecticide	**carbamate**
	Chloronil	fungicide	
	Nu Cop	fungicide-bactericide	
Mixture #5	Caparol	herbicide	
	Lorox	herbicide	
	Volunteer	herbicide	
	Permethrin 3.2	insecticide	**pyrethroid**

Table 1.2. Pesticide schedule for two celery fields on one Michigan celery farm in 2014. Mix numbers correspond to those specified in Table 1.1.

Field 1

Week	Date	Mixture	Insecticide class	Reason for application
1	31-May	Mix #5	pyrethroid	Weeds/Aster leafhopper
1	5-Jun	Mix #2	organophosphate	Aster leafhopper
3	17-Jun	Mix #4	carbamate	Aster leafhopper/Tarnished plant bug
4	25-Jun	Mix #5	pyrethroid	Weeds/Aster leafhopper
5	30-Jun	Mix #4	carbamate	Aster leafhopper/Tarnished plant bug
6	8-Jul	Mix #1	pyrethroid	Aster leafhopper
7	17-Jul	Mix #2	organophosphate	Aster leafhopper/Tarnished plant bug
8	23-Jul	Mix #5	pyrethroid	Weeds/Aster leafhopper
9	31-Jul	Mix #2	organophosphate	Tarnished plant bug/Aphids
10	8-Aug	Mix #3	organophosphate	Tarnished plant bug/Caterpillars
12	20-Aug	Mix #1	pyrethroid	Tarnished plant bug/Caterpillars

Field 2

Week	Date	Mixture	Insecticide class	Reason for application
1	7-Jun	Mix #4	carbamate	Aster leafhopper/Tarnished plant bug
4	25-Jun	Mix #5	pyrethroid	Weeds/Aster leafhopper
5	30-Jun	Mix #4	carbamate	Aster leafhopper/Tarnished plant bug
5	2-Jul	Mix #5	pyrethroid	Weeds/Aster leafhopper
6	8-Jul	Mix #1	pyrethroid	Aster leafhopper
7	17-Jul	Mix #2	organophosphate	Aster leafhopper/Tarnished plant bug
9	31-Jul	Mix #2	organophosphate	Tarnished plant bug/Aphids
10	8-Aug	Mix #3	organophosphate	Tarnished plant bug/Caterpillars
12	20-Aug	Mix #1	pyrethroid	Tarnished plant bug/Caterpillars

CHAPTER 2:

The spatial and temporal distribution of pests and natural enemies in Michigan commercial celery systems

Introduction

Celery (*Apium graveolens* L.) is a biennial plant in the Apiaceae, grown commercially as an annual, and selected for its large succulent petioles. It was first established as a commercial crop in the United States during the late nineteenth century in Kalamazoo, MI (Berger *et al.* 1988, Levine 2013). Michigan currently accounts for 5.5% of total U.S. celery production with 98.5 million pounds harvested from 1700 acres and a market value of just under $19 million (USDA NASS, 2015). Although most of the production in Michigan occurs in the southwest region of the state, there is notable acreage in the west central and eastern counties as well.

Most, if not all, commercial celery production in Michigan occurs on muck soils (Zandstra *et al.* 1986, Wong *et al.* 2010), which are remnant geographic water features that have dried out due to natural processes, lowering of the local water table through ground water withdrawal, or have been intentionally drained for cultivation (Brady & Weil 2007, Lindbo and Kozlowski 2005). Muck soils have high organic matter content, high water retention capacity, and low bulk density, which are desirable attributes for growing transplantable crops (Lindbo and Kozlowski 2005). Field sizes and shapes for celery in southwest Michigan vary based on the total area of muck soil available at any particular location and range from small pond-size "pockets" of muck to remnant lake and river beds covering hundreds of acres. While installing drainage technology in small pockets is economically prohibitive, in large areas of muck, growers will often construct and install a network of drainage ditches and tiling to lower the water table across the entire area (J. Jubenville pers. obs., Brady and Weil 2007, Lindbo and

Kozlowski 2005). While the widths of these large fields are based on individual grower equipment, they are often ~50m wide (J. Jubenville, pers. observation). Consequently, celery farms in southwest Michigan tend to have long, narrow fields (e.g. 400-800m x 50m) that are bordered on two or three sides by drainage ditches (Figs 1.2A-B).

Ditches are bordered on both sides by weedy marginal areas that vary in width, but are usually about 2 meters wide and managed by mowing or herbicide application. Mowing occurs, on average, once per month during the season; herbicide application usually happens just before transplanting and can be the only margin management needed for the life of the crop (R. Eding. pers. comm., Zandstra 1986, Fig 1.3A-B). In addition, growers will often leave cultivated, plant-free soil as a buffer zone between margins and the crop. This buffer zone results in a "hard" visual interface between the lush green crop, the dark muck soil, and the weedy margin-ditch area (Fig. 1.4A-B).

Major pests of celery include aphids (*Aphis spiraecola, A. helianthi, Myzus persicae*), the tarnished plant bug (*Lygus lineolaris*), the aster leafhopper (*Macrosteles quadrilineatus*), and the variegated cutworm (*Peridroma saucia*). Minor pests include the two-spotted spider mite (*Tetranychus urticae*), the carrot weevil (*Listronotus oregonensis*), and thrips (Thysanopetera: Thripidae). The celery leaftier (*Udea rubigalis*), along with slugs, leafminers (Diptera: Agromyzidae), and loopers (Lepidoptera: Noctuidae) can cause damage in large numbers, but are best described as sporadic pests in Michigan celery fields.

Knowledge of the typical spatial and temporal abundance patterns exhibited by any particular pest is essential for designing efficient and conscientious pest management programs. Apart from occasional extension bulletins, published descriptions of insects in Michigan celery are sparse. Reference material regarding community composition and relative abundance at the

field, local, and regional scale is lacking. Constructing and maintaining an inventory of arthropods across a sizable geographic area allows us to document and monitor taxa of interest and determine whether fluctuations in abundance are synchronous across the region. Moreover, determining field-scale spatiotemporal distribution patterns may allow growers to implement site-specific management practices in which insecticides are applied only to targeted locations within a field. Practices such as these could lower production costs and reduce the environmental impact of commercial agriculture in these potentially sensitive ecosystems. Providing a within-field refuge from pesticides may also help to conserve natural enemies and could result in more consistent pest control throughout the season (e.g. Morrison and Szendrei 2013).

I studied the celery arthropod community as managed by experienced growers on established farms with a history of continuous celery production. The purpose of this study is to document the relative abundance and spatiotemporal distribution of arthropods within the canopy of commercial celery crops in Michigan in order to determine important groups and detect aggregative tendencies. Special emphasis is placed on key pests and natural enemies.

Materials and Methods

Study sites. Each growing season (2013 and 2014), I selected three commercial celery farms based on geographic separation and grower willingness to participate in cooperative research projects. In 2013, farms were located in Ottawa, Allegan, and Van Buren counties and were separated by distances that ranged from 23.4 km to 85.6 km (mean distance: 57.6 km). In 2014, farms were located in Allegan and Van Buren counties with a geographical separation ranging from 35.2 km to 72.2 km (mean distance: 57.0 km). Two of the farms participated both years, resulting in a total of four farms over the course of two seasons. Two newly transplanted fields

from each farm were selected for sampling, which resulted in a total of six fields per season. Fields on the same farm were selected to be as far apart as possible. Sampling side of the field was bordered by a drainage ditch whenever possible (~83% of study fields).

Sampling methods. I sampled canopy arthropods using yellow sticky traps placed at canopy level. I established three transects that were arranged perpendicular to and spatially equidistant along the field edge and extended from the weedy margins into the field. Transect length was uniform and determined by the distance between the edge and the middle of the most narrow field. Four fixed sampling positions were located along each transect at the following points: the margin, the crop edge, 10 meters into the crop, and 25 meters into the crop for a total of twelve traps per field (Fig 2.1). I used non-baited 7.6 by 12.5 cm yellow sticky traps (Great Lakes IPM,

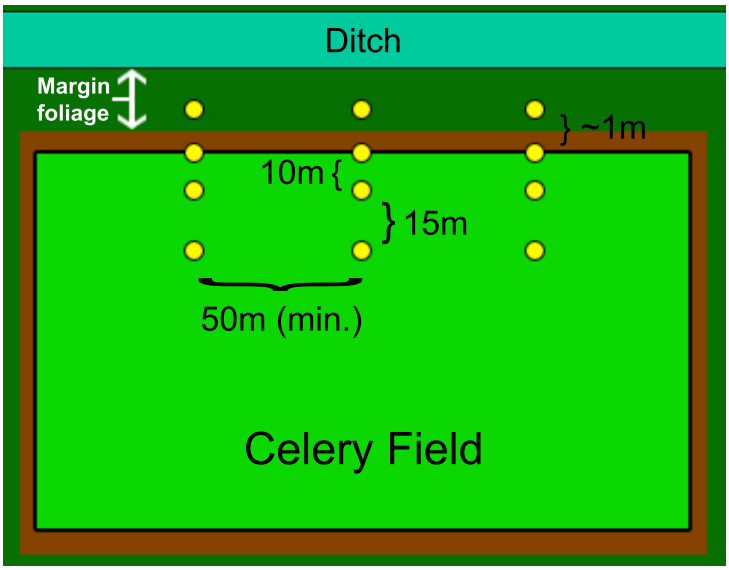

Figure 2.1. Generalized canopy sampling design. Transects for yellow sticky traps were established in six commercial celery fields located in three southwest Michigan counties in 2013 and 2014. Yellow dots denote sampling locations.

Vestaburg, MI) placed at canopy level with wire loop hangers. During the first month, the canopy was low and I simply inserted the hangers into the soil. However, as the plants grew taller, I used 76.2 x 1.3 cm galvanized pipe to extend the length of the hanger and raise the traps to canopy level. Traps were replaced weekly between late May and early September in both 2013 and 2014. Arthropods of interest were counted and identified to the lowest possible taxonomic unit. Two specific groups were not counted as natural enemies during the 2013 season: Dolichopoidae (Diptera) and *Scymnus* spp. (Coleoptera: Coccinellidae). Thus, I only present data on these taxa for the 2014 season.

Statistical analysis. I used R (R Core Team, 2014) and *glmmADMB* (Skaug, Fournier, Bolker, Magnussin, and Nielsen 2014) to perform a multilevel mixed-model Poisson regression of the relationship between distance from the edge and arthropod abundance. Data were subset and analyzed by week to accommodate distributional assumptions and improve the fit of the model. Sampling position was entered as a fixed effect. For random effects, I entered intercepts for farm, field, and transect, all of which were nested to account for spatial autocorrelation (transect within field within farm). Model selection and probability distributions (poisson, negative binomial, zero-inflated, etc.) were based on AIC criteria and Pearson's dispersion coefficient (Hilbe 2014). To test for significance of the fixed effect, I performed likelihood ratio tests of the full model against a model without the effect. Taxonomic groups were analyzed individually. Statistical separation of mean abundance between sampling positions was performed by post-hoc analysis using Tukey's HSD ($\alpha = 0.05$). In cases where weekly counts of a taxonomic group were consistently too low to analyze, I pooled the data by month or by season. As a rule, I tried to

analyze the data in as many temporal subsets as possible in order to obtain the finest resolution of spatial distribution possible across the season.

I analyzed overall seasonal abundance by pooling weekly data and performing a mixed-model linear regression of sampling position against arthropod abundance in R using *lme4* (Bates, Maechler, Bolker, and Walker, 2014). Sampling position, week, and the interaction of sampling position and week were entered as fixed effects. As before, farm, field, and transect were specified as nested random effects. Data were transformed ($\log_e$+1) to improve model fit and meet distributional assumptions of normality and homoscedasticity. To test for significance of the two fixed effects and their interaction, I iteratively dropped the interaction and effects from the model and performed likelihood ratio tests against the full model. P-values are reported in Table 2.1. Taxonomic groups were analyzed individually. Statistical separation of mean abundance between sampling positions was performed by post-hoc analysis using Tukey's HSD ($\alpha = 0.05$).

Results

Overview. I recorded a total of 73,366 and 118,185 arthropods in 2013 and 2014, respectively, for a grand total of 191,551 captured arthropods (Table S1). The total herbivore counts were 62,987 in 2013 and 106,928 in 2014 and accounted for 85.9% and 90.5% of yearly captures, respectively. The total number of predators was 3,060 in 2013 and 4,424 in 2014, accounting for 4.2% and 3.7% of the yearly captures, respectively. Finally, I counted 5,622 parasitoids in 2013 and 6587 in 2014, which accounted for 7.7% and 5.6% of yearly captures respectively.

Spatio-temporal distribution of pests.

Aphids. Aphids were the most abundant pest group captured in both years, accounting for 45.8% and 57% of all counted herbivores in 2013 and 2014, respectively (Table S1). A total of 28,893 and 60,938 adult aphids were captured on yellow sticky traps in 2013 and 2014, respectively. Aphid abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=16.04$, $P<0.001$). In both years, mean aphid numbers remained relatively low during the first nine weeks of the season, but started to increase substantially around mid-August and continued to increase every week until the crop was harvested (Figs. 2.2A-B & S1).

Seasonal abundance patterns: Overall in 2013, aphids displayed a margin-centric pattern with ≈48% more aphids captured in the margins and ≈40% more captured at the field edge than at either interior position (Fig. 2.5A). The overall influence of sampling position was statistically significant (Sample position (S): $\chi^2(3)=50.26$, $P<0.001$; Fig. 2.2A), as well as the interaction with time (Sample position (S) x Time (T): $\chi^2(36)=56.11$, $P=0.018$; Figs. 2.2A & S1).

Overall in 2014, the margin-centric pattern was not repeated. Instead, mean aphid capture was greatest at the 10m position, with ≈35% more aphids captured than in the margins and ≈25% more than either of the other field positions (Fig. 2.5B). Although the influence of sampling position was statistically significant for the season (S: $\chi^2(3)=34.95$, $P<0.001$; Fig. 2.2B), as well as the interaction with time (SxT: $\chi^2(33)=73.11$, $P<0.001$; Figs. 2.2B & S1), the differences between the overall means were not statistically separable with post hoc Tukey's HSD pair-wise comparison (Fig. 2.5B).

Weekly abundance patterns: Aphids were usually more abundant at the field edge than at the other positions during the first 5 weeks of 2013 (Fig. S1); sample position significantly influenced aphid abundance during this time (Table 2.1). Differences among positions were less

apparent during the next three weeks despite significant differences in weeks 7 and 8 (Table 2.1). Sampling position was not a significant predictor of aphid abundance during the final five weeks, although there appears to be a slight margin-oriented trend in weeks 12 and 13 (Fig. S1, Table 2.1).

Aphid abundance was significantly influenced by sampling position during weeks 2-8 in 2014 (Table 2.1). Mean margin captures were always among the most abundant, with numbers generally decreasing with distance into the field (Fig. S1). Relatively speaking, these numbers are low compared with the last month of the 2014 season in which abundance increased sharply every week (Figs. 2.2B & S1). Similar to 2013, sampling position was not a significant predictor for late-season aphid abundance. The final week of 2014 was an exception, however, with aphid abundance significantly higher 10m into the field (Table 2.1, Fig. S1).

***Thrips*.** Thrips were the second most abundant pest group captured in both years, accounting for 37.2% and 26.9% of all counted herbivores in 2013 and 2014, respectively (Table S1). A total of 23,483 and 28,736 thrips were captured on yellow sticky traps in 2013 and 2014, respectively. The majority of thrips were likely onion thrips, *Thrips tabaci*, but were too numerous to consistently identify in a timely manner. Thrips abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=59.60$, $P<0.001$). In both years, thrips abundance was low to start the season, but increased dramatically during the first month (Figs. 2.1C-D). There were three noticeable peaks in abundance during the 2013 season: late June, mid-July, and mid-August. Thrips abundance during the 2014 season peaked in late June, decreased over the next three weeks and remained relatively low for the rest of the season (Fig. 2.1D & Fig. S2).

Seasonal abundance patterns: Overall in 2013, thrips displayed an even distribution pattern across all sampling locations (Fig. 2.5C). The overall influence of sampling position was not statistically significant (S: $\chi^2(3)=0.57$, P=0.905); neither was the overall interaction with time (SxT: $\chi^2(36)=29.51$, P=0.769). Overall in 2014, thrips were evenly distributed across all sampling locations within the crop, but significantly more abundant in the margins (Fig. 2.5D). In total, 56.4%, 40.2%, and 38.1% more thrips were captured in the margins than at the edge, 10m, and 25m positions, respectively. The overall influence of sampling position was statistically significant (S: $\chi^2(3)=24.15$, P<0.001), as well as the interaction with time (SxT: $\chi^2(33)=55.69$, P=0.008, Figs. 2.5D & Fig. S2). Season mean thrips captures were 65.8%, 47.3%, and 45.1% greater in the margins than they were at the edge, 10m, and 25m positions, respectively (Figs. 2.1D & 2.5D).

Weekly abundance patterns: Mean abundance within weeks was similar among all positions in 2013 (Fig. S4). With exception of the last week of June, sample position did not significantly influence thrips abundance (Table 2.1). By contrast, the edge position was almost always among the most abundant positions for weekly mean thrips captures in 2014. Within the crop, sample position significantly influenced thrips abundance in weeks 4, 6, and 9, although the differences were small (Fig. S2, Table 2.1). Mean margin abundance was 73-94% greater than the other positions during the first half of the season, but often statistically indistinguishable from the others during the second half (Figs. 2.2D & S2, Table 2.1). By and large, thrips were evenly distributed across all positions during the second half of the season (Figs. 2.1D & S2).

Potato leafhopper. Potato leafhoppers (PLH) were the 3rd most abundant pest group captured in both years, accounting for 5.7% and 6.1% of all counted herbivores in 2013 and 2014,

respectively (Table S1). A total of 3,582 and 6,524 adult PLH were captured on yellow sticky traps in 2013 and 2014, respectively. Potato leafhopper abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=117.83$, $P<0.001$). In both years, mean PLH abundance peaked in late June and early July; there was an additional peak at the end of the 2013 season (Fig. 2.2G-H & Fig. S3).

Seasonal abundance patterns: Overall, in 2013, PLH were evenly distributed across all locations within the crop, but were significantly less abundant in the margins (Fig. 2.5G). In total, ~46% more PLH were captured on the field edge than at the other two crop locations and ~71% more PLH were captured at the edge than in the margins. The overall influence of sampling position was statistically significant (S: $\chi^2(3)=26.00$, $P<0.001$), as well as the interaction with time (SxT: $\chi^2(36)=90.081$, $P<0.001$, Figs. 2.5G & Fig. S3). Mean PLH captures were ~15% greater at the 10m and 25m positions and 65% greater at the edge position than they were in the margins (Figs. 2.2G & 2.5G).

In 2014, the capture totals for the margins and field edges were the greatest out of all sampling positions as well as being nearly identical. In total, ~32% and ~62% more PLH were captured at either the edge or the margin positions than at the 10m and 25m positions, respectively. The overall influence of sampling position was statistically significant (S: $\chi^2(3)=45.30$, $P<0.001$), but the interaction with time was not (SxT: $\chi^2(33)=27.09$, $P=0.756$, Figs. 2.5H & Fig. S3).

Weekly abundance patterns: In all but the last three weeks of the season, PLH were evenly distributed across all three positions within the crop in 2013 (Fig. S3, Table 2.1). During the final two weeks, mean PLH abundance increased notably at the edge position, but remained stable at the other two interior positions. Weekly mean margin abundance was statistically

indistinguishable from the edge for seven out of the 12 weeks. In weeks 4,5,6, and 13, however, there were statistical differences in the number of PLH caught between margin and the field edge, ~1m apart. In total, sampling position significantly influenced PLH abundance in 8 out of the twelve weeks (Fig. 2.2G, Table 2.1).

Potato leafhoppers were, for the most part, evenly distributed for the first month of the 2014 growing season. The trend during the six weeks following peak abundance was edge-oriented, with abundance decreasing with distance into the field (Fig. S3). The trend was similar in the last two weeks, but the differences were not statistically significant (Table 2.1). As previously mentioned, mean and total abundance for PLH in the margin and edge positions were nearly identical in 2014 (Figs. 2.2H & S3).

Aster leafhopper. Aster leafhoppers (ALH) were the 4th most abundant pest group captured in both years, accounting for 3.5% and 3.9% of all counted herbivores in 2013 and 2014, respectively (Table S1). A total of 2,190 and 4,174 adult ALH were captured on yellow sticky traps in 2013 and 2014, respectively. Aster leafhopper abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=20.42$, $P<0.001$). In both years, ALH numbers were highest during the first month of the crop, steadily declined during the second month, and remained relatively low during the final month (Fig. 2.2 E-F & Fig. S4).

Seasonal abundance patterns: Overall in 2013, ALH displayed an even distribution pattern across all sampling locations (Fig. 2.5E). In total, 14.5% more ALH were captured on the edge of the crop than at any other sampling position. The overall influence of sampling position was not statistically significant (S: $\chi^2(3)=5.81$, $P=0.121$, Fig. 2.2E), and neither was the interaction with time (SxT: $\chi^2(36)=48.91$, $P=0.071$). Overall in 2014, ALH displayed an even distribution

across all locations within the crop, but were significantly less abundant in the margins (Fig. 2.5F). In total, ~22% more ALH were captured on the edge than at the other two field locations and ~102% more were captured at the edge than in the margins. The overall influence of sampling position was statistically significant (S: $\chi^2(3)=9.98$, P=0.019), as well as the interaction with time (SxT: $\chi^2(33)=81.88$, P<0.001, Figs. 2.2F & S4). Mean ALH captures were ~60% greater at the 10m and 25m positions and ~90% greater at the edge position than they were in the margins (Figs. 2.5F).

Weekly abundance patterns: The edge position was always among the most abundant positions for weekly mean ALH captures in 2013. Within the crop, sample position significantly influenced ALH abundance in weeks 1, 6, 11, and 13, although the differences were often small (Fig. S2, Table 2.1). Mean margin abundance was often similar to the edge position, but was significantly smaller in weeks 3 & 4 (Fig. S4, Table 2.1). In total, sampling position significantly influenced ALH abundance 6 out of 12 analyzable weeks in 2013 (Table 2.1).

In all but two weeks of the season (weeks 9 & 11), aster leafhoppers were evenly distributed across all three positions within the crop in 2014 (Fig. S4). In three of the first four weeks, when ALH were most abundant, mean abundance in the margins was significantly less than in the crop (Fig. 2.2F & S4). During the second and third months, however, mean ALH abundance in the margins was usually not significantly different than any other sampling position (Fig. S4, Table 2.1).

Tarnished plant bug. Tarnished plant bugs (TPB) were the 10th most abundant pest group captured in 2013 and the 7th most abundant pest group captured in 2014, accounting for 1% and 0.6% of all counted herbivores in 2013 and 2014, respectively (Table S1). They are included in

this analysis due to their historical importance as a polyphagous crop pest. A total of 210 and 742 adult TPB were captured on yellow sticky traps in 2013 and 2014, respectively. Tarnished plant bug abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=142.4$, $P<0.001$). In both years, TPB numbers were lowest during the first month of the crop, increased slightly during the second month, and were highest during the last month (Fig. 2.2I-J & Fig. S5). Capture numbers were low during 2013 and had to be pooled by month for analysis.

Seasonal abundance patterns: Overall in 2013, TPB displayed an even distribution pattern across all sampling locations (Fig. 2.5I). The overall influence of sampling position was not statistically significant (S: $\chi^2(3)=0.46$, $P=0.927$); neither was the interaction with time (SxT: $\chi^2(36)=44.91$, $P=0.147$). Overall in 2014, TPB were evenly distributed across all sampling locations within the crop, but significantly more abundant in the margins (Fig. 2.5J). In total, 64.9%, 81.6%, and 133% more TPB were captured in the margins than at the edge, 10m, and 25m positions, respectively. The overall influence of sampling position was statistically significant (S: $\chi^2(3)=31.30$, $P<0.001$), but the interaction with time was not (SxT: $\chi^2(33)=44.06$, $P=0.095$, Figs. 2.5J & Fig. S5).

Weekly abundance patterns: Due to low numbers in 2013, weekly TPB captures were pooled across months for analysis. The influence of sampling position did not influence abundance during any month of 2013 (July: $\chi^2(3)=3.04$, $P=0.386$; August: $\chi^2(3)=4.07$, $P=0.254$, Table 2.1). Twice as many individuals were captured at the interior field positions for the month of July (Fig 2.1I). In August, the pattern was reversed; more TPB were captured in the margins and edge than in the interior field positions (Fig. 2.1I).

In all but one week of the season, tarnished plant bugs were evenly distributed across all three positions within the crop in 2014 (Figs. 2.1J, S5). The margin position was always among the most abundant positions for weekly TPB captures. During the first five weeks, there were no differences in mean abundance between the margin and all other positions. The following seven weeks, as overall numbers began to increase, TPB were usually more abundant in the margins than the other positions (Figs. 2.1J, S5). Sampling position was a significant predictor of TPB abundance during weeks 6-9 and had a marginally significant effect during week 11 (Table 2.1, Fig. S5).

Spatiotemporal distribution of natural enemies.

***Spiders*.** Spiders were the most abundant predator, accounting for 24.5% and 26.3% of all captured predators in 2013 and 2014 (Table S1). A total of 747 and 1,088 spiders were captured on yellow sticky traps in 2013 and 2014, respectively. Spider abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=28.37$, $P<0.001$). In both years, mean spider numbers were relatively low during the first month of the season, but started to increase around the beginning of July (Fig 2.3A-B & Fig. S6). Abundance peaked in the third week of July in 2013 and began to steadily decrease and then stabilize at lower numbers around the second week of August (Fig 2.3). In 2014, there was a relatively large amount of variation in abundance within and between weeks, especially after the first month. The trend was generally upwards starting in early July and reached a dynamic period of peak abundance between weeks 7-11 and then sharply decreased in week 12 (Fig. 2.3B & Fig. S6).

Seasonal abundance patterns: Overall in 2013, spiders displayed an even distribution pattern across all sampling locations (Fig. 2.6A). In total, 52%, 74.5%, and 55.7% more spiders were

captured at the edge position than at the margin, 10m, and 25m positions, respectively. Seasonal mean spider captures were 46.9%, 72%, and 52.4% greater on the edges than they were at the margin, 10m, and 25m positions, respectively (Fig. 2.6A & Fig. S6). However, the overall influence of sampling position was not statistically significant (S: $\chi^2(3)=4.79$, P=0.188); neither was the overall interaction with time (SxT: $\chi^2(36)=20.80$, P=0.980).

Likewise, in 2014, spiders were evenly distributed overall (Fig 2.6B). In total, 44.6%, 48.9%, and 34.1% more spiders were captured at the 25m position in than at the margin, edge, and 10m positions, respectively. Although the influence of sampling position was statistically significant for the season (S: $\chi^2(3)=9.43$, P=0.024), as well as the interaction with time (SxT: $\chi^2(33)=52.51$, P=0.017; Figs. 2.3B & S6), the differences between the overall means were not statistically separable with post hoc Tukey's HSD pair-wise comparison (Fig. 2.6B).

Weekly abundance patterns: In all but the week of peak abundance in 2013, spiders were evenly distributed across all sampling locations (Fig. S6). With the exception of the third week of July, sample position did not significantly influence spider abundance (Table 2.2). The differences during that week were relatively high, with mean edge abundance 87.5-173% greater than the other positions (Figs. 2.3A & S6). In contrast to 2013, the 25m position was among the most abundant positions for weekly mean spider captures in 2014 (Figs. 2.3B & S6). Sample position influenced spider abundance in weeks 5, 10, and 11; spiders were evenly distributed across positions the other nine weeks of 2014 (Table 2.2).

Coleomegilla maculata. Of the coccinellids captured, *Coleomegilla maculata* (CMAC) was the most abundant, accounting for 82.8% and 52.1% of captured lady beetles in 2013 and 2014, respectively (Table S1). A total of 347 and 263 adult CMAC were captured on yellow sticky traps in 2013 and 2014, respectively. CMAC abundance was not significantly influenced by year

(multilevel mixed-model linear regression, year: $\chi^2(1)=1.25$, P=0.269). In both years, CMAC numbers were highest during the first month of the crop and then decreased as time progressed (Fig. 2.3C-D). Because capture numbers were low for both seasons, data were subset and analyzed by month.

Seasonal abundance patterns: Overall in 2013, CMAC displayed an even distribution pattern across all sampling locations (Fig. 2.6C). Seasonal mean CMAC captures were 34.4%, 22.9%, and 17.8% greater in the margins than they were at the edge, 10m, and 25m positions, respectively (Fig. 2C). However, the overall influence of sampling position was not statistically significant (S: $\chi^2(3)=3.31$, P=0.346); neither was the overall interaction with time (SxT: $\chi^2(36)=36.65$, P=0.439). Overall in 2014, CMAC were evenly distributed over all sampling positions (Fig 2.6D). Total capture was greatest at the edge and 25m positions; the totals were very similar (101 & 103, respectively) In total, ≈44% and ≈15% more CMAC were captured at the edge or 25m positions than at the margin and 10m positions in 2014. The overall influence of sampling position was not statistically significant (S: $\chi^2(3)=2.33$, P=0.506); neither was the overall interaction with time (SxT: $\chi^2(33)=20.53$, P=0.956). Sampling position did not influence abundance for any month during 2014 (Fig 2.6C-D, Table 2.2).

Syrphidae. Hover flies were the 6th most abundant predatory group captured in 2013 and the 9th most abundant in 2014 (Table S1). They are included here due to their historical and ecological importance as highly-mobile cosmopolitan generalist predators. A total of 288 and 127 adult syrphids were captured on yellow sticky traps in 2013 and 2014, respectively. Syrphid abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=34.37$, P<0.001). In both years, syrphid numbers were low in early June, peaked in July

and slowly declined over the month of August (Fig. 2.6E-F). Because capture numbers were low for both seasons, data were subset and analyzed by month.

Seasonal abundance patterns: Overall in 2013, syrphids displayed an even distribution across all sampling locations (Fig. 2.6E). Season mean syrphid captures were 40.4%, 71.2%, and 78% greater in the margins than they were at the edge, 10m, and 25m positions, respectively (Fig. 2.6E). The influence of sampling position was statistically significant (S: $\chi^2(3)=16.89$, $P<0.001$) for the season; but the interaction with time was not (SxT: $\chi^2(36)=25.60$, $P=0.901$). Conversely, sampling position did not significantly influence abundance during any month in 2013 (Fig. 2.3E, Table 2.2).

Overall in 2014, syrphids displayed an even distribution across all locations within the crop, but were significantly more abundant in the margins than in the interior field positions (Fig. 2.6F). Seasonal mean syrphid captures were 75.6%, 153%, and 178% greater in the margins than they were at the edge, 10m, and 25m positions, respectively (Fig. 2.6F). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=17.1$, $P<0.001$), but the interaction with time was not (SxT: $\chi^2(33)=21.71$, $P=0.934$, Fig. 2.3F). The differences between the overall means were statistically separable with post hoc Tukey's HSD pair-wise comparison ($\alpha=0.05$; Fig. 2.6F). Furthermore, sampling position was found to influence abundance in July and August of 2014 (Fig. 2.3F, Table 2.2).

Chalcidoidea. Wasps in the superfamily Chalcidoidea were the most abundant group of parasitoids captured in both seasons, accounting for 46.9% and 54.3% of all captured parasitoids in 2013 and 2014, respectively (Table S1). A total of 1,958 and 3,581 chalcidoid wasps were captured on yellow sticky traps in 2013 and 2014, respectively. Chalcidoid abundance was

significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=130.32$, $P<0.001$). In both years, mean chalcidoid numbers dipped considerably in the second week compared to the first week, then increased continuously until their first peak period in second week of July (Fig 2.4A-B). Populations in both years dipped again and then began to increase at a relatively high rate around the third week of August and continued in that fashion until the crop was harvested.

Seasonal abundance patterns: Overall in 2013, chalcidoid wasps displayed an even distribution across all locations within the crop, but were significantly more abundant in the margins (Fig. 2.7A). Total mean chalcidoid margin captures were greater than those at the edge, 10m, and 25m positions by factors of 2.17, 2.73, and 2.85, respectively (Fig 2.7A). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=86.1$, $P<0.001$), as well as the interaction with time (SxT: $\chi^2(36)=54.50$, $P=0.025$, Figs. 2.4A & S7).

Overall in 2014, chalcidoid wasps were most abundant in the margins, and far less abundant at the field positions (Fig. 2.7B). Total mean chalcidoid margin captures were greater than those at the edge, 10m, and 25m positions by factors of 2.93 5.51, and 7.47, respectively (Figs. 2.4B & 2.7B). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=352.8$, $P<0.001$), as well as the interaction with time (SxT: $\chi^2(33)=66.25$, $P<0.001$, Figs. 2.7B & S7).

Weekly abundance patterns: The margin position was always among the most abundant positions for weekly mean chalcidoid captures in 2013 (Fig. 15). In seven out of the 13 weeks, chalcidoids were distributed evenly across all three positions within the crop. The differences in abundance in the other six weeks, while statistically significant, were often small (Table 2.2, Fig.

S7). In total, sampling position significantly influenced chalcidoid abundance in all but one week (week 8) in 2013 (Table 2.2).

Likewise, on a weekly basis, chalcidoids were always most abundant in the margins in 2014. During the first five weeks, chalcidoid abundance was evenly distributed across all three field locations. However, during weeks 6-12, abundance at the field edge was usually significantly higher than in the interior positions (10m & 25m). In total, sampling position significantly influenced chalcidoid abundance every week in 2014 (Table 2.2).

Mymaridae. Mymarid wasps were the second most abundant group of parasitoids captured in both seasons, accounting for 22.6% and 24.1% of all captured parasitoids in 2013 and 2014, respectively (Table S1). A total of 946 and 1591 mymarids were captured on yellow sticky traps in 2013 and 2014, respectively. Mymarid abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=124.06$, $P<0.001$). No mymarids were found the first three weeks of 2013. Starting in week four, there was considerable variation from week to week in 2013 (Fig 2.4C). Although peak numbers were reached in week 10, they were also relatively high in weeks 5, 7, and 13. By comparison, weekly numbers were relatively stable and consistent in 2014. Although mean mymarid abundance peaked in week 9, those numbers were not considerably larger than many other weeks of the season (Fig. 2.5D).

<u>*Seasonal abundance patterns*</u>: Overall in 2013, mymarid wasps displayed an even distribution across all locations within the crop, but were significantly more abundant in the margins (Fig. 6C). Total mean mymarid margin captures were greater than those at the edge, 10m, and 25m positions by factors of 1.96, 2.3, and 2.82, respectively (Figs. 2.4C & 2.7C). The overall

influence of sampling position was statistically significant (S: $\chi^2(3)=80.89$, $P<0.001$), as well as the interaction with time (SxT: $\chi^2(36)=80.65$, $P<0.001$, Figs. 2.4C & S8).

Overall in 2014, mymarid wasps were once again most abundant in the margins, and evenly distributed across all three field positions (Fig. 2.7D). Total mean mymarid margin captures were greater than those at the edge, 10m, and 25m positions by factors of 1.77, 2.34, and 2.32, respectively (Figs. 2.4D & 2.7D). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=86.85$, $P<0.001$), but the interaction with time was not (SxT: $\chi^2(33)=42.06$, $P=0.1$, Fig. 2.4D & Fig. S8).

Weekly abundance patterns: The margin position was always among the most abundant positions for weekly mean mymarid captures in 2013 (Fig. S8). Mymarids were distributed evenly across all three positions within the field in three out of ten weeks. The differences in abundance in the other seven weeks, while statistically significant, were often small (Table 2.2, Fig. S8). In total, sampling position significantly influenced mymarid abundance in all but two weeks (weeks 4 & 11) in 2013 (Table 2.2).

As in the previous year, mymarids were always most abundant in the margins on a weekly basis in 2014. In six out of the 12 weeks, mymarids were distributed evenly across all three positions within the field. Abundance patterns during the other six weeks were usually edge-centric (Table 2.2, Fig. S8). In total, sampling position significantly influenced mymarid abundance eight out of 12 weeks in 2014 (Table 2.2).

Trichogrammatidae. Trichogrammatid wasps were the 4th most abundant group of parasitoids captured in both seasons, accounting for 4.4% and 6.8% of all captured parasitoids in 2013 and 2014, respectively (Table S1). A total of 185 and 448 trichogrammatid wasps were captured on yellow sticky traps in 2013 and 2014, respectively. Trichogrammatid abundance was

significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=95.72$, $P<0.001$). In both years, wasp numbers were lowest in the first month and increased continuously over the following two months (Fig 2.4E-F). Because capture numbers were low for both seasons, data were subset and analyzed by month.

Seasonal abundance patterns: Overall in 2013, trichogrammatids had an edge-centric distribution pattern (Fig. 2.7E) with mean captures being 9.25%, 29.2%, and 102% greater in the margins than they were at the edge, 10m, and 25m positions, respectively (Figs. 2.4E & 2.7E). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=7.96$, $P=0.047$) as well as interaction with time (SxT: $\chi^2(36)=56.03$, $P=0.018$). When subset by month, sampling position did not influence abundance for either month in 2013 (Fig 2.4E, Table 2.2). Overall in 2014, trichogrammatid wasps were most abundant in the margins and decreased in abundance with increasing distance into the field (Fig. 2.7F). Season mean trichogrammatid captures were 22.5%, 90.4%, and 131% greater in the margins than they were at the edge, 10m, and 25m positions, respectively (Figs. 2.4E & 2.7E). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=29.06$, $P<0.001$), but the interaction with time was not (SxT: $\chi^2(33)=28.20$, $P=0.705$, Figs. 3E). When subset by month, sampling position was found to influence abundance in July and August of 2014 (Fig. 2.4F, Table 2.2).

Braconidae. Braconid wasps were the 5th most abundant group of parasitoids captured in 2013 and the 3rd most abundant group captured in 2014, accounting for 4.4% and 7.9% of all captured parasitoids in their respective years (Table S1). A total of 184 and 520 braconids were captured on yellow sticky traps in 2013 and 2014, respectively. Braconid abundance was significantly influenced by year (multilevel mixed-model linear regression, year: $\chi^2(1)=166.9$, $P<0.001$). In

both years, wasp numbers were relatively stable across the whole season with peaks appearing in early-mid July and late August (Fig 2.4G-H). Because capture numbers were low in 2013, data were subset and analyzed by month for that year.

Seasonal abundance patterns: Overall in 2013, braconid wasps displayed an even distribution across all locations within the crop, but were significantly more abundant in the margins (Fig. 2.7G). Season mean braconid margin captures were greater than those at the edge, 10m, and 25m positions by factors of 1.89, 3.66, and 3.26, respectively (Figs. 2.4G & 2.7G). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=37.71$, $P<0.001$), as well as the interaction with time (SxT: $\chi^2(36)=56.03$, $P=0.018$). When subset by month, sampling position was found to influence abundance for all three months of 2013 (Fig. 2.4G, Table 2.2).

Overall in 2014, braconid wasps were most abundant in the margins and displayed a slight edge-centric pattern in the field (Fig. 2.7H). Season mean braconid margin captures were greater than those at the edge, 10m, and 25m positions by factors of 2.37, 3.54, and 3.77, respectively (Figs. 2.4H & 2.7H). The overall influence of sampling position was statistically significant (S: $\chi^2(3)=130.4$, $P<0.001$), but the interaction with time was not (SxT: $\chi^2(33)=37.78$, $P=0.260$, Fig. 2.4H & Fig. S9).

Weekly abundance patterns: The margin position was always among the most abundant positions for weekly mean braconid captures in 2014 (Fig. S9). Braconid wasps were distributed evenly across all three positions within the crop in nine out of twelve weeks. Abundance patterns during the other three weeks were edge-centric (Table 2.2, Fig. S9). In total, sampling position significantly influenced braconid abundance in eight weeks in 2014 (Table 2.2).

Table 2.1. Significance of fixed effect (sample position) on weekly or monthly herbivore abundance in commercial celery fields in southwest Michigan during 2013 and 2014. ALH - aster leafhopper, PLH - potato leafhopper, TPB - tarnished plant bug.

Taxon	2013				2014			
Aphid	**week**	**df**	**Chisq**	***P***	**week**	**df**	**Chisq**	***P***
	1	3	40.84	<0.001	1	3	3.212	0.360
	2	3	35.71	<0.001	2	3	12.84	0.005
	3	3	26.89	<0.001	3	3	25.19	<0.001
	4	3	29.89	<0.001	4	3	13.17	0.004
	5	3	25.2	<0.001	5	3	45.94	<0.001
	6	3	5.51	0.138	6	3	35.73	<0.001
	7	3	10.49	0.015	7	3	26.76	<0.001
	8	3	10.94	0.012	8	3	12.8	0.005
	9	3	6.61	0.085	9	3	3.838	0.279
	10	3	4.906	0.179	10	3	4.352	0.226
	11	3	3.322	0.345	11	3	7.094	0.069
	12	3	4.962	0.175	12	3	12.77	0.005
	13	3	4.746	0.191				

Taxon	2013				2014			
Thrips	**week**	**df**	**Chisq**	***P***	**week**	**df**	**Chisq**	***P***
	1	3	196.6	<0.001	1	3	7.062	0.070
	2	3	4.285	0.232	2	3	20.62	<0.001
	3	3	5.76	0.124	3	3	32.27	<0.001
	4	3	9.34	0.025	4	3	15.52	0.001
	5	3	64.37	<0.001	5	3	27.49	<0.001
	6	3	0.886	0.829	6	3	12.26	0.007
	7	3	1.957	0.581	7	3	4.866	0.182
	8	3	0.662	0.882	8	3	2.194	0.533
	9	3	5.634	0.131	9	3	9.813	0.020
	10	3	5.544	0.136	10	3	5.49	0.139
	11	3	6.252	0.1	11	3	7.239	0.065
	12	3	1.808	0.613	12	3	6.146	0.105
	13	3	3.32	0.345				

ALH	**week**	**df**	**Chisq**	***P***	**week**	**df**	**Chisq**	***P***
	1	3	9.009	0.029	1	3	23.93	<0.001
	2	3	6.576	0.091	2	3	8.656	0.034
	3	3	12.39	0.006	3	3	2.216	0.529
	4	3	8.064	0.045	4	3	22.33	<0.001
	5	3	2.046	0.563	5	3	10.92	0.012
	6	3	12.25	0.007	6	3	4.076	0.253
	7	3	8.944	0.030	7	3	3.506	0.320
	8	3	2.349	0.503	8	3	4.733	0.192
	9	3	3.759	0.289	9	3	15.65	0.001
	10	3	3.786	0.286	10	3	6.71	0.082
	11	3	9.257	0.026	11	3	8.23	0.042
	12			NA	12	3	11.07	0.011
	13	3	15.64	0.001				

PLH	**week**	**df**	**Chisq**	***P***	**week**	**df**	**Chisq**	***P***
	1			NA	1	3	0.942	0.815
	2	3	16.62	<0.001	2	3	10.27	0.016
	3	3	4.862	0.182	3	3	2.296	0.513
	4	3	21.26	<0.001	4	3	6.39	0.094
	5	3	50.25	<0.001	5	3	16.04	0.001
	6	3	34.29	<0.001	6	3	19.66	<0.001
	7	3	2.248	0.523	7	3	12.14	0.007
	8	3	4.54	0.209	8	3	23	<0.001
	9	3	3.994	0.262	9	3	9.328	0.025
	10	3	13.14	0.004	10	3	10.53	0.015
	11	3	9.462	0.024	11	3	7.25	0.064
	12	3	18.64	3E-04	12	3	6.104	0.107
	13	3	16.18	0.001				

TPB	**month**	**df**	**Chisq**	***P***	**week**	**df**	**Chisq**	***P***
	1			NA	1			NA
	2	3	3.036	0.386	2			NA
	3	3	4.066	0.254	3	3	0.873	0.832
					4	3	4.679	0.197
					5	3	4.719	0.194
					6	3	19.51	<0.001
					7	3	16.51	<0.001
					8	3	26.17	<0.001
					9	3	20.36	<0.001
					10	3	4.088	0.252
					11	3	7.764	0.051
					12	3	1.542	0.673

Table 2.2. Significance of fixed effect (sample position) on weekly or monthly natural enemy abundance in commercial celery fields in southwest Michigan during 2013 and 2014. CMAC-*Coleomegilla maculata*.

Taxon	2013				2014			
CMAC	month	df	Chisq	*P*	month	df	Chisq	*P*
	1	3	3.958	0.266	1	3	1.674	0.643
	2	3	0.866	0.834	2	3	5.774	0.123
	3	3	0.098	0.992	3	3	0.28	0.964
Aranae	week	df	Chisq	*P*	week	df	Chisq	*P*
	1			NA	1	3	3.963	0.265
	2	3	1.359	0.715	2	3	6.813	0.078
	3	3	4.543	0.208	3	3	7.858	0.049
	4	3	4.525	0.210	4	3	1.47	0.689
	5	3	3.236	0.357	5	3	11.77	0.008
	6	3	4.738	0.192	6	3	5.631	0.131
	7	3	14.15	0.003	7	3	4.366	0.225
	8	3	3.776	0.287	8	3	1.132	0.769
	9	3	6.014	0.111	9	3	2.639	0.451
	10	3	3.219	0.359	10	3	18.34	0.000
	11	3	1.313	0.726	11	3	8.858	0.031
	12	3	1.965	0.580	12	3	6.481	0.090
	13	3	3.198	0.362				
Mymaridae	week	df	Chisq	*P*	week	df	Chisq	*P*
	1			NA	1	3	12.02	0.007
	2			NA	2	3	20.09	<0.001
	3			NA	3	3	39.07	<0.001
	4	3	7.062	0.070	4	3	6.292	0.098
	5	3	30.53	<0.001	5	3	61.29	<0.001
	6	3	18.56	<0.001	6	3	16.25	0.001
	7	3	30.75	<0.001	7	3	7.926	0.048
	8	3	9.814	0.020	8	3	6.35	0.096
	9	3	17.85	<0.001	9	3	13.45	0.004
	10	3	14.69	0.002	10	3	14.19	0.003
	11	3	3.675	0.299	11	3	11.5	0.009
	12	3	10.74	0.013	12	3	10.25	0.017
	13	3	18.56	<0.001				
Trichogramm.	month	df	Chisq	*P*	month	df	Chisq	*P*
	1			NA	1	3	3.798	0.284
	2	3	2.92	0.404	2	3	9.012	0.029
	3	3	7.094	0.068	3	3	19.72	0.000

Taxon	2013				2014			
Syrphidae	month	df	Chisq	*P*	month	df	Chisq	*P*
	1	3	6.516	0.089	1	3	53.12	0.150
	2	3	1.326	0.723	2	3	10.33	0.016
	3	3	2.644	0.450	3	3	10.27	0.016
Chalcidoidea	week	df	Chisq	*P*	week	df	Chisq	*P*
	1	3	24.55	<0.001	1	3	37.17	<0.001
	2	3	19.72	<0.001	2	3	21.39	<0.001
	3	3	30.4	<0.001	3	3	50.3	<0.001
	4	3	11.15	0.011	4	3	44.95	<0.001
	5	3	23.14	<0.001	5	3	35.94	<0.001
	6	3	21.77	<0.001	6	3	40.5	<0.001
	7	3	20.1	<0.001	7	3	17.31	<0.001
	8	3	4.98	0.173	8	3	23.2	<0.001
	9	3	10.9	0.012	9	3	43.03	<0.001
	10	3	9.452	0.024	10	3	58.26	<0.001
	11	3	55.5	<0.001	11	3	48.57	<0.001
	12	3	47.58	<0.001	12	3	55.41	<0.001
	13	3	111.2	<0.001				
Braconidae	month	df	Chisq	*P*	week	df	Chisq	*P*
	1	3	21	<0.001	1	3	46.08	<0.001
	2	3	20.7	<0.001	2	3	45.73	<0.001
	3	3	7.858	0.049	3	3	6.924	0.074
					4	3	43.59	<0.001
					5	3	29.8	<0.001
					6	3	21.64	<0.001
					7	3	4.347	0.226
					8	3	11.79	0.008
					9	3	11.01	0.012
					10	3	5.632	0.131
					11	3	19.74	<0.001
					12	3	0.352	0.950

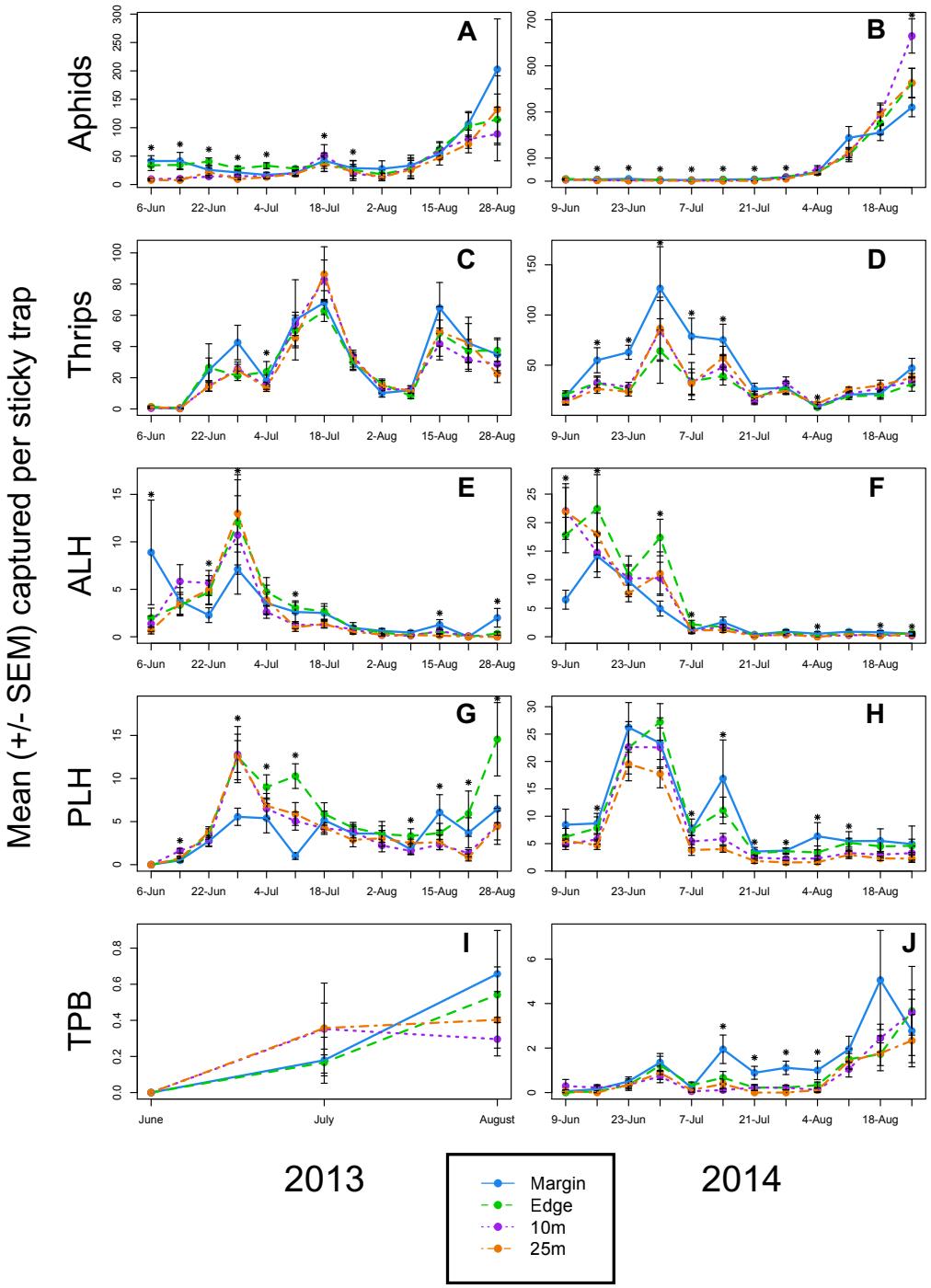

Figure 2.2. Weekly or monthly mean abundance (±SEM) of herbivores captured in the celery canopy with yellow sticky traps at different distances into the field for 2013 and 2014. Asterisks indicate significant differences among sampling positions within a particular week ($\alpha = 0.05$). ALH - aster leafhopper, PLH - potato leafhopper, TPB - tarnished plant bug.

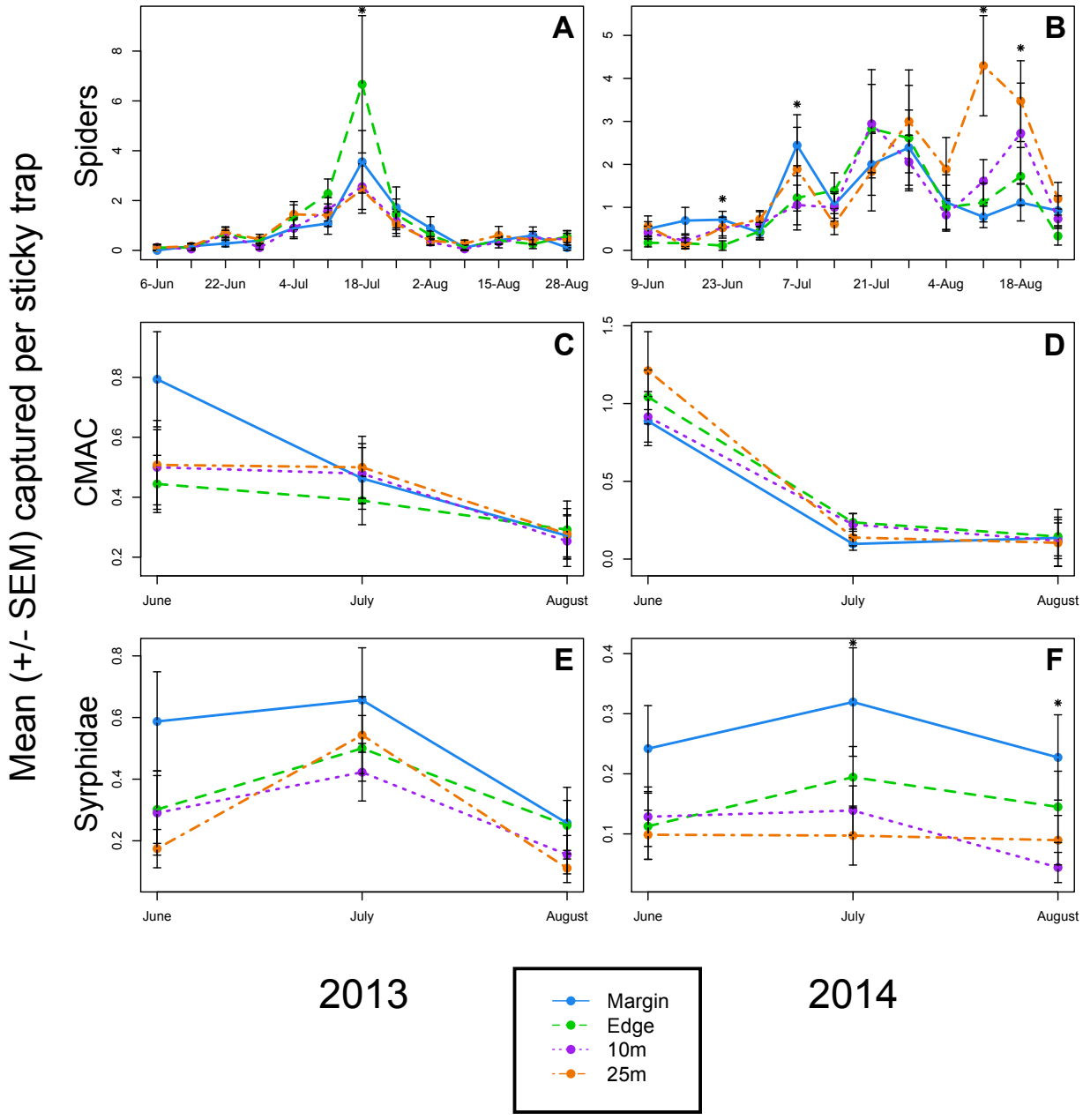

Figure 2.3. Weekly or monthly mean abundance (±SEM) of predators captured in the celery canopy with yellow sticky traps at different distances into the field for 2013 and 2014. Asterisks indicate significant differences among sampling positions within a particular week ($\alpha = 0.05$). CMAC - *Coleomegilla maculata*.

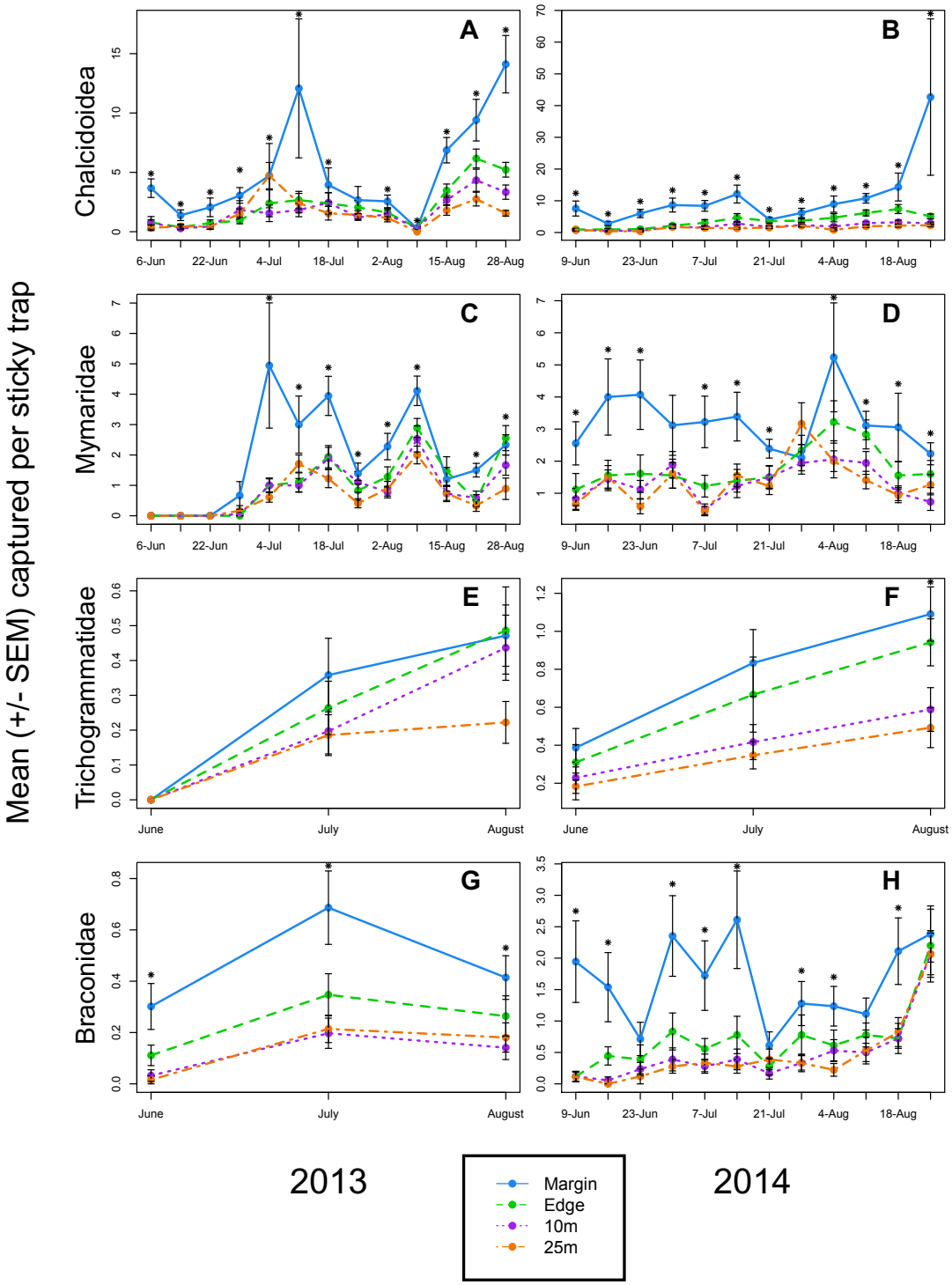

Figure 2.4. Weekly mean abundance (±SEM) of parasitoids captured in the celery canopy with yellow sticky traps at different distances into the field for 2013 and 2014. Asterisks indicate significant differences among sampling positions within a particular week ($\alpha = 0.05$).

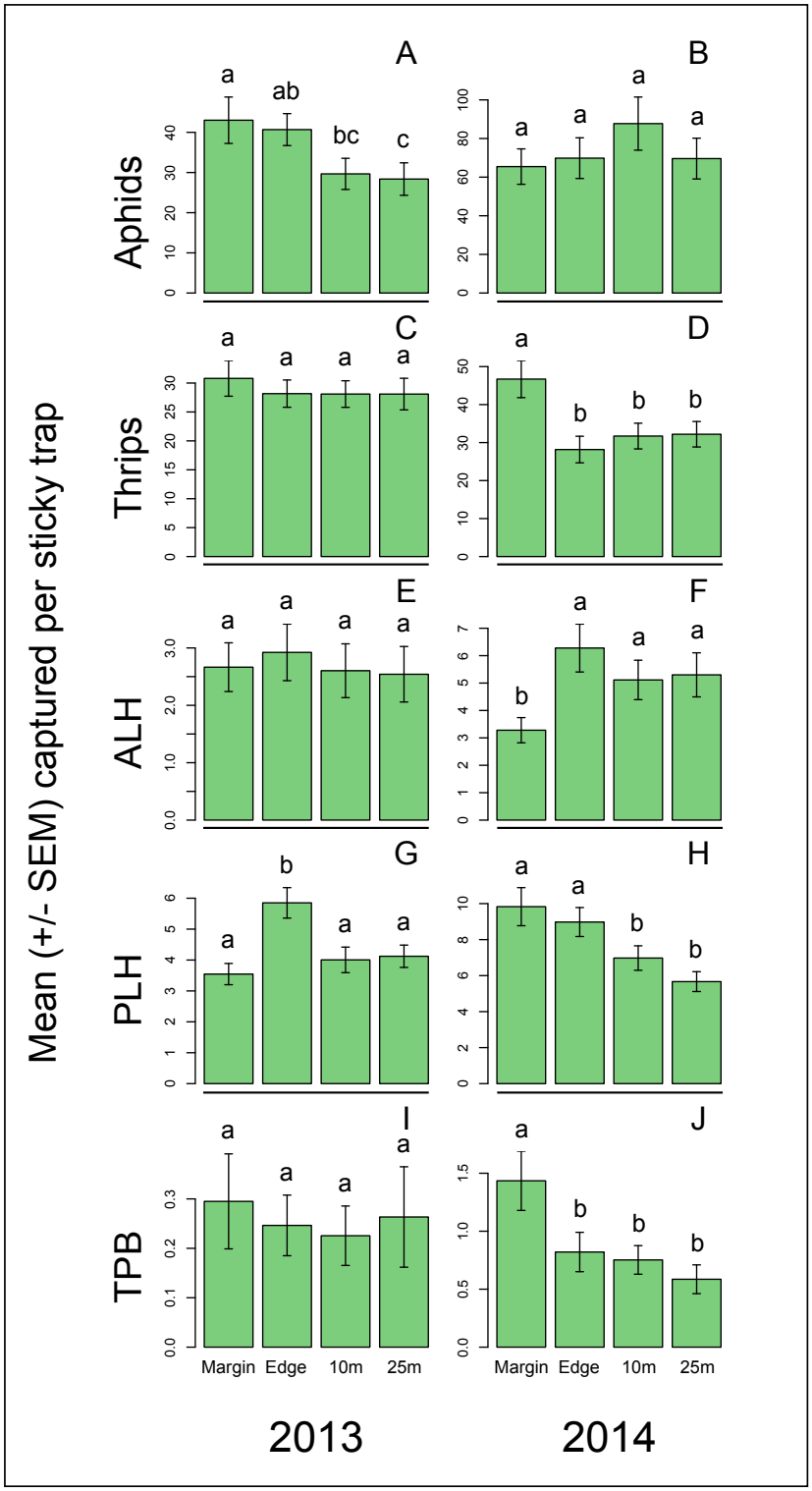

Figure 2.5. Overall (seasonal) mean abundance (±SEM) of herbivores at different distances into the field for 2013 and 2014 seasons. Bars with the same letter within the same year are not significantly different (Tukey's HSD; $\alpha = 0.05$). ALH - asterleafhopper, PLH - potato leafhopper, TPB - tarnished plant bug.

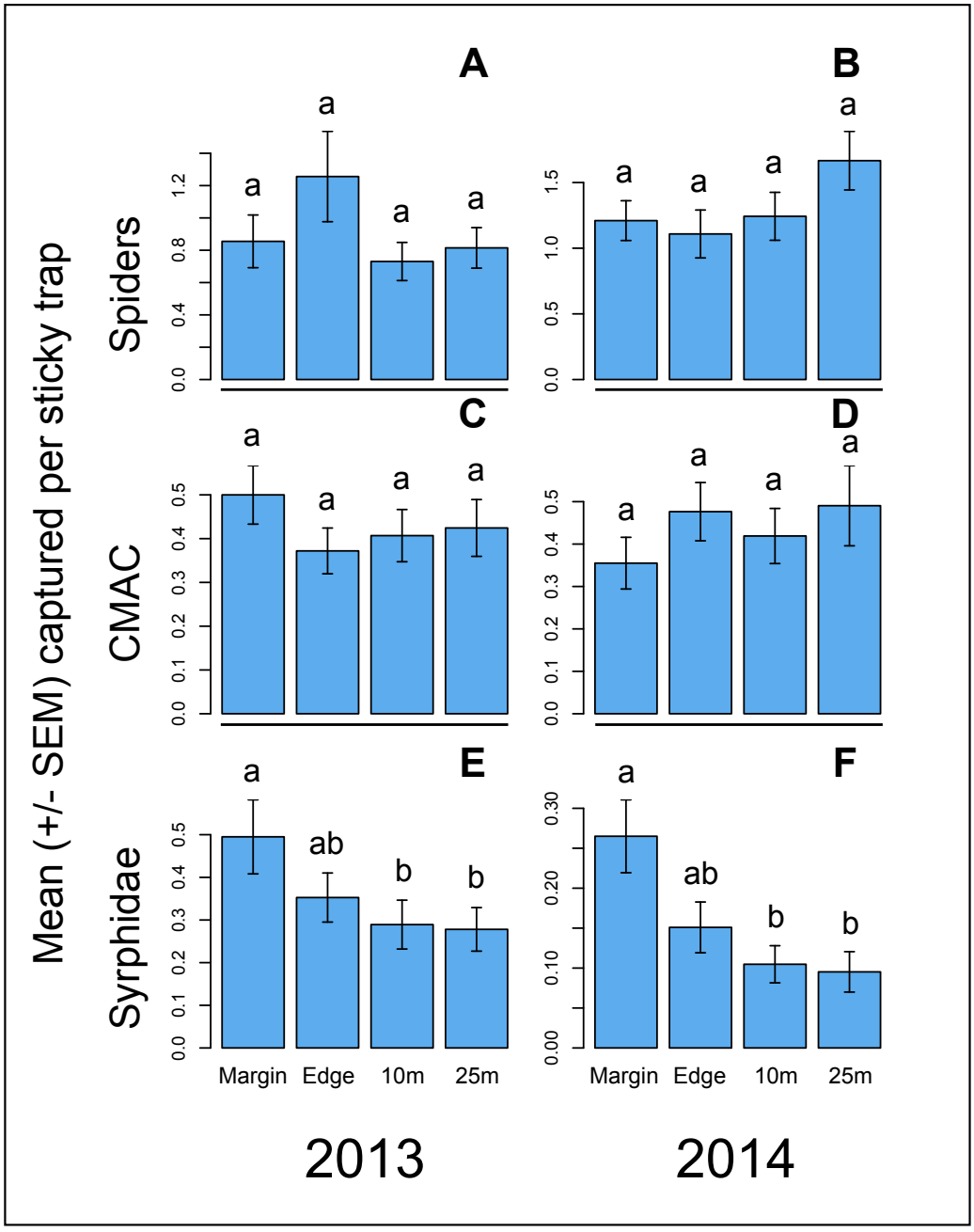

Figure 2.6. Overall (seasonal) mean abundance (±SEM) of predators at different distances into the field for 2013 and 2014 seasons. Bars with the same letter within the same year are not significantly different (Tukey's HSD; $\alpha = 0.05$). CMAC - *Coleomegilla maculata*.

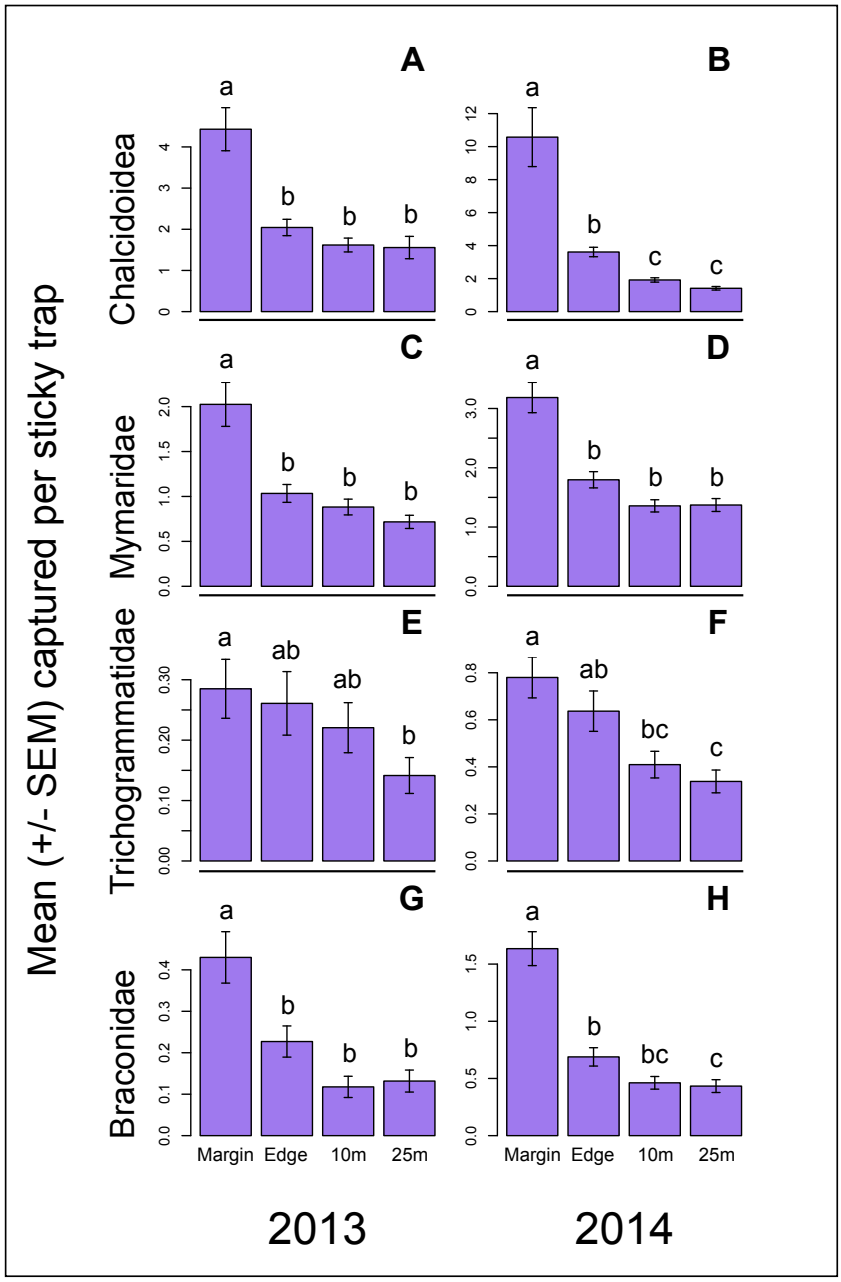

Figure 2.7. Overall (seasonal) mean abundance (±SEM) of parasitoids at different distances into the field for 2013 and 2014 seasons. Bars with the same letter within the same year are not significantly different (Tukey's HSD; $\alpha = 0.05$).

Discussion

In general, most captured arthropods were distributed evenly across the crop and were more abundant in the margins just outside the field. Edge effects were often detected when abundance was low, but usually disappeared when abundance was near the seasonal peak. Furthermore, persistence of these patterns across the season varied according to group.

Aphids. Aphid abundance was greater on the edges and margins of celery fields during the first half of the season in both years when relative abundance was low. When abundance was higher, later in the seasons, aphids were evenly distributed throughout the field. Organisms across a broad taxonomic range have been shown to be able to detect and respond to habitat edges (Haddad 1999, Haddad et al. 2003). Herbivorous pests have the tendency to aggregate initially on the edges of agricultural fields (van Helden 2010). The suggested reason for this behavior is that the pest first locates the crop (habitat location) from the air, drops below the flight boundary layer and proceeds to locate a host plant (Taylor 1974, van Helden 2010). The host location process usually results in the insect encountering the edge of the crop and then stopping. Michigan celery fields often have a sharp crop-soil interface (Fig. 1.4), which may influence host location and aggregation in certain pest groups. Aphids have been found to aggregate at the edges of other crops after insecticide application, but may only be detectable at scales larger than 25m (Winder *et al.* 1999). For example, Winder *et al*. (1999) concluded that the edge effects for *Sitobion avenae* in winter wheat extended from 30 to 60 meters into the field with constant density throughout. Because the margins are not directly sprayed with insecticides, these areas may function as small refuge strips for arthropods. Aphids (and many other groups) that I caught on sticky traps likely came from two places: margins or the aerial plankton pool. Aerial plankton

is the collective name for the pool of tiny organisms that fly or drift on atmospheric wind currents and include small light-bodied arthropods like spiders and aphids. I expected to catch more aphids at the field edge at the early stages of re-colonization due to normal foraging/host-location activity of surviving herbivores from the margins. If the wind-borne aphids are low in abundance, then foraging patterns from the margin may be detectable, even at such a small scale. However, when aphid abundance grows exponentially later in the season, the sheer number of wind-transported aphids will easily mask small edge effects from residual aphid populations left in the margins after the most recent insecticide application. Thus, it is likely that the vast majority of aphids caught in the celery canopy have not come directly from the margins.

Thrips. Thrips abundance was greatest from late June to mid-July in both 2013 and 2014. Thrips were found in relatively consistent numbers across all field positions in both years. In 2014, a minor negative edge effect was seen in the spatial distribution plot (Fig. S4) which shows more thrips were caught in the center of the field than at the edges (Figure S4). A possible explanation for this is that the center of the fields may experience reduced natural enemy activity due to population depletion from insecticide application. Overall, margin abundance was often highly similar to that found in the celery field itself.

Potato leafhopper. Potato leafhoppers were more abundant during the first half of the season with peak numbers usually occurring in late June or early July. Comparatively, this occurs at approximately 1-2 weeks later than the aster leafhopper. Although it is not cited as a disease vector, the stereotypical stunting and necrosis caused by PLH feeding ("hopperburn") can cause

tremendous damage to a field of young transplants (Capinera 2001). For this reason, chemical management of leafhoppers in newly-transplanted fields should extend into early July.

The within-field distribution of potato leafhoppers was fairly consistent between the two years. In general, more PLH were found on the edges of the celery field than within the interior, although they were often evenly distributed within fields when numbers were relatively high (Fig. S3). This pattern is consistent with other studies in alfalfa (Emmen *et al.* 2004) and soybeans (Poston and Pedigo 1975), although the fields of those crops are typically much larger than celery fields. Abundance in the margins, relative to the field locations, was not consistent between 2013 and 2014. PLH have been shown to develop successfully on pigweed (*Amaranthus spp.*) and smartweed (*Polygonum* spp.) (Capinera 2001), both of which grow readily in celery field margins. Consequently, a reasonable explanation for margin-centric abundance patterns may be directly linked to the presence and vegetative growth stage of preferred weed hosts outside the celery field.

Aster leafhopper. Aster leafhoppers were evenly distributed across the celery crop in both 2013 and 2014. Similarly to aphids, a faint edge effect was detected when relative abundance was low, but this was not observed when abundance was high. Unlike the aphids, ALH abundance was often lower in the margins during periods of peak abundance. One explanation for this is that margins are often mowed or sprayed with herbicide around the time of planting, when seasonal ALH abundance is at its peak. As a result, there are fewer resources to exploit in those areas. Oviposition site selection behavior may also factor into these patterns. Aster leafhoppers overwinter as eggs in grasses and weeds (Meade and Peterson, 1964), but spring and summer generations may prefer to reproduce in the celery field (or other vegetable crop) where plants are

growing rapidly and the vascular fluids are highly nutritious. Another potential explanation is that ALH may be disinclined to cross the boundary of the field edge (van Helden 2010), especially if a sharp (bare soil) interface exists between the field and the margin.

Tarnished plant bug. Tarnished plant bug populations increased with time and were evenly distributed throughout celery fields during both growing seasons. These insects are highly-mobile foragers that can easily disperse over 25m within seconds (J. Jubenville, pers. obs.). Margin abundance was usually similar to or greater than abundance within the field. Tarnished plant bugs are true generalists and readily exploit weedy margins in other crops (Snodgrass *et al.* 1984, Young 1986, Capinera 2001, Snodgrass *et al.* 2005, Outward *et al.* 2008); margin management should be a priority in systems where TPB is a pest.

Spiders. Spiders were consistently the most abundant predators found on canopy traps, although their distribution and the abundance within the field was highly variable from week to week. Overall, they were evenly distributed across celery fields. The vast majority of these spiders were immatures, and although I was unable to indentify them to family, they were likely Linyphiid spiders, due to the great abundance of sheet webs consistently found throughout celery fields (J. Jubenville, pers. obs.). These spiders disperse in the winds by ballooning and are not thought to be capable of directed flight (Suter 1999). As such, their distribution in the field should be strongly influenced by how the wind breaks on hedgerows and other tall objects (buildings, etc.) near the field. Due to their abundance, field penetration, persistence, and generalist diet, spiders are probably one of the most important predators in these systems. Any possibility of reaping

natural pest control services from this group, however, is likely reduced by near-weekly insecticide applications to the field.

***Coleomegilla maculata*.** The most abundant coccinellid in celery systems is *Coleomegilla maculata* (CMAC). They can be found in similar abundance at any location in the field or margin. Because they experience the landscape on a scale much larger than 25m, an even distribution is to be expected. No edge effects were detected.

Coleomegilla maculata is notable among coccinellids for a truly polyphagous diet. Gut content analysis has shown that they ingest pollen and fungal spores in addition to other arthropods (Webber and Lundgren 2009). One implication is that they can sustain themselves with alternative resources while arthropod prey are temporarily absent from agricultural fields. Conserving refuge habitat near the field could have a positive effect on CMAC abundance in the field (Landis *et al*. 2000).

Syrphidae. Syrphid flies were evenly distributed throughout the field. Like CMAC, syrphids are highly mobile generalist predators that likely experience the landscape at greater distances than the size of an average celery field in this study. Because of their great vagility, one might expect them to be equally abundant across all locations. Syrphid abundance, however, was consistently greater in the margins and decreased with distance into the field (Figure 2.6). One explanation might be that margins are managed less frequently, harbor a greater diversity of flora, and likely serve as a refuge for alternative prey. Syrphid larvae are predatory, making the margin a preferable habitat for oviposition over celery fields that are often devoid of prey. Another potential explanation is that weeds in the margins and ditch banks occasionally reach the

flowering stage. Because nectar is an important floral resource for adult syrphids, they likely prefer margins over flower-less celery fields (Hickman and Wratten 1996). In celery margins, syrphid adults have frequently been seen feeding on the flowers of smartweed (J. Jubenville, pers. obs.). As with CMAC, it is likely that creating habitat with flowering resources near the field could have a positive effect on syphid abundance within these systems (Cowgill *et al.* 1993, Landis *et al*. 2000).

Parasitoids. Edge effects, while variable across groups, were apparent and persistent among parasitoids as a whole. Chalcidoid and braconid wasps were evenly distributed across the field in 2013, but clearly more abundant on the field edge in 2014. Mymarid wasps were evenly distributed in both years, but showed a non-significant trend of decreasing abundance with increasing distance into the field. Trichogrammatid wasps displayed a margin-centric abundance pattern in both years, but this was more pronounced in 2014.

In all cases, parasitoid abundance was notably greater in the margins than at any field location across the whole season. Dipteran species were present in great abundance in these systems, especially near the ditches. It is likely that these species served as hosts to some of the chalcidoids that I captured. Because margins can be, to a certain extent, considered refuges from insecticides, populations residing in these areas are never depleted. This is could also be a reason for the sheer numerical dominance of Chalcidoids, among parasitoids.

If parasitoid populations were maintained within the margins, then the edge effects I observed can be explained as a result of foraging behavior into the fields from these areas. In previous studies, parasitoids have been observed to remain in the general area of patches where they have had recent success in locating hosts (e.g. Waage 1978, 1979, Cronin 2009). Moreover,

the probability for the parasitoid returning to a patch seems to increase with exposure to a host chemical stimulus (Waage 1978). As margins are likely to be refuges for hosts, this might explain the persistent margin-centric abundance pattern. Longley *et al*. (1997) reported similar re-colonization patterns of parasitoids after insecticide treatment in winter wheat fields. The patterns they reported, however, were short-lived and disappeared after 5 days. Interestingly, they also reported that overall, primary parasitoid populations within the crop were below pre-spray levels 5 days after application with numbers near the field center still recovering after 12 days. Given that celery fields are sprayed with insecticides on a near-weekly basis, our results are quite similar to Longley *et al*. (1997) and could be explained as a product of the pest management regime. Because adult parasitoids derive their nourishment largely from nectar, enriching refuge areas with floral resources could have a positive effect on parasitoid longevity and abundance (Wackers 2001, 2004; Winkler *et al*. 2009).

Synthesis. Migration movement in insects has been defined as directed movement while temporarily ignoring typical host location cues (Kennedy 1985). Even insect groups that are considered weak fliers, such as whiteflies, can travel several kilometers with directed flight upwind over a period of hours (Byrne 1999). In this context, the distance between the edge and the center of many celery fields should not be difficult for most canopy arthropods to move across in a directed manner within a matter of seconds. As the results here show, however, different groups display different distribution patterns. Differences in distribution patterns may be indicative of differences in the source of these captured insects. A margin-centric pattern, one in which abundance is greatest in the margin and decreases with distance, suggests that the particular taxon is using the margin as habitat. Whereas a distribution pattern in which

abundance is uniform across all sampling locations (i.e. there is no central position of greatest abundance) carries no such suggestion.

Most of the herbivore groups I sampled were evenly distributed across all four sampling locations. Small edge effects were detected in some groups when relative abundance was low, but the practical significance may be minimal. Leafhoppers were occasionally less abundant in the margins. This behavior may have to do with host availability and habitat preference.

Predators were also evenly distributed across all field locations. Of the predators, syrphid flies were the only group with significantly more individuals captured in the margins. Factors that likely contribute to this behavior are the availability of alternative resources and refuge within the margins. On the whole, parasitoids were also more abundant in the margins. Mymarids were evenly distributed throughout the field, while braconid, chalcidoid, and trichogrammatid wasps displayed clear edge effects. As with the syrphids, alternative resources and refuge within the margins likely play a role in this pattern.

Knowledge of spatial and temporal patterns of insect pests in agricultural fields can be useful for designing efficient scouting protocols, estimating pest densities, and developing management strategies that eliminate unnecessary pesticide application (Winder *et al*. 1999). My results suggest that sampling on the edge will generally capture the same number of individuals as sampling from the center of most fields. However, there are many celery fields in southwest Michigan that are wider than the fields we sampled and therefore may have different distribution patterns. Considering the small edge effects detected at 25m, I would expect that the effect would be more distinguishable in wider fields.

The relationship between herbivores and the margins varies across groups. My results suggest that in some cases, the margins are used for resources and that these areas could serve as

a source for recolonizing the fields after insecticide application (e.g. tarnished plant bugs). Both leafhoppers (ALH, PLH) are known to feed and develop on weedy margin species (Wallis 1962, Capinera 2001, Frost *et al*. 2011) commonly found in celery systems. With this in mind, it seems likely that leafhopper and tarnished plant bug populations would benefit from unmanaged margins and that current margin management practices limit their populations near the crop.

Although current margin management practices dampen pest populations, they are also likely limiting the populations of important groups of natural enemies. Based on my results, it is likely that the Chalcidoidea, Mymaridae, Braconidae, Trichogrammatidae, and Syrphidae would all benefit from conserving the vegetative structure within margins and ditch banks. These groups all have member species that are known to attack the suite of celery pests highlighted in this study and practices that promote stability and growth in their populations may benefit growers in the form of increased pest control (Landis *et al*. 2000). Nevertheless, while the idea of conserving and managing margins is intriguing, additional research is necessary to determine whether the net effect would be beneficial or simply a breeding ground for serious celery pests (Winkler *et al*. 2010).

CHAPTER 3:

The movement of arthropods between margin and field in Michigan celery agroecosystems

Introduction

Land use within the modern agricultural landscape falls along a continuum of habitat stability, with areas of intense disturbance on one end and near-natural areas at the other. At the farm scale, crop fields are ephemeral habitats that experience frequent and intense disturbance while border areas are often managed less frequently and with varying levels of intensity. Pest management practices often eliminate arthropods within the field, but border areas are not usually managed in this way. The inequality in disturbance between adjacent areas may result in a source-sink dynamic with arthropods from border habitats re-colonizing the suddenly unoccupied field. Because local abundance can be influenced by factors at the landscape scale, it should not be assumed that margins are the primary source of insects within the field. Understanding the source of beneficial and pestiferous insects within an agricultural production system is fundamental to selecting the most suitable management practices.

Michigan celery is grown on muck soils, which occur naturally in lowland swampy areas. Growers will often construct and install a network of drainage ditches and tiling to lower the water table across the entire area of muck soil. A common result of this strategy is an aggregation of long narrow fields across the muck area, each bordered on two or three sides by drainage ditches. Ditches are bordered on both sides by weedy marginal areas that vary in width, but are usually about 2m wide and managed by mowing or herbicide application. These marginal areas are reminiscent of "beetle banks" which provide a refuge for ground beetles and other arthropods from intense agricultural practices that might otherwise kill them (Landis et al. 2000).

Conserving beneficial arthropods along refuge strips may result in greater pest control and fewer pesticide applications (Landis *et al.* 2000). In many ways, the field-margin-ditch configuration in celery systems appears to be an ideal (albeit, unintentional), implementation of this concept. Many celery fields are narrow, with their centers approximately 25 meters from the edge. Re-colonization of such narrow fields should be expected to happen quickly once the toxicity of pesticide residues begins to fade. In an earlier chapter I showed that arthropods from most taxonomic groups show little difference in abundance between the edge and the center of celery fields (CHAPTER 2). However, some of these groups are most abundant in the margins, indicating that border habitat in these systems could be serving as both a refuge and a source (CHAPTER 2).

Ecological models predict herbivore abundance will be higher in the center than at the edge of large cereal fields due to predation pressure from the outside (Bianchi and van der Werf 2004). Empirical support of this prediction has been in shown in studies where natural enemy abundance is greater on the edge than the center, while herbivore abundance is greater in the center than the edge after insecticide applications (Duffield & Aebischer 1994, Longley *et al*. 1997). This makes intuitive sense as predator and parasitoid populations generally track herbivore populations over time. Many celery fields, however, are considerably smaller than cereal fields (only 50m wide on average), thus natural enemies should quickly track herbivores to the middle of the field. Furthermore, if margins in these systems are managed for the conservation of arthropods, an increase in certain natural enemy populations could result in elevated natural pest control. In combination with accurate population estimation, economic thresholds, and regular scouting, this would be the foundation of an integrated pest management

strategy to reduce the ecological impact of intensive farming while maintaining economic viability.

An undesirable outcome, however, is that herbivore populations will also increase as a result of conserving margin vegetation. The presence of alternative prey is generally viewed as a necessity for maintaining stability in local natural enemy populations whenever prey within the crop disappear as a result of insecticide application (Altieri 1999, Landis *et al*. 2000). All of the aforementioned pests (CHAPTER 2) are known to be polyphagous, some with a dietary niche ranging across hundreds of plant species (Wallis 1962, Young 1986, Capinera 2001, Blackman & Eastop 2007, Frost *et al*. 2011). In particular, the tarnished plant bug has a documented reputation as a "border species" that readily inhabits weedy margins (Snodgrass *et al.* 1984, Young 1986, Capinera 2001, Snodgrass *et al.* 2005, Outward *et al.* 2008). Evaluating the extent to which arthropod species interact with the margins, then, is a necessary first step in assessing the potential viability of a margin conservation strategy in Michigan celery.

A related issue in this regard is whether natural enemies found within non-crop habitats move into the crop to forage for prey or hosts. The movement patterns of natural enemies between crop and non-crop habitat is often poorly understood and results in a general inability to predict and evaluate the efficacy of habitat management for improved pest control (Lavendero *et al*. 2004, Synder *et al.* 2005, but see Schellhorn *et al*. 2014). Therefore, it has been recommended, that future studies examine, among other things, the movement patterns of insects between focal areas in addition to their overall abundance (Synder *et al.* 2005).

Recently, an improved method for marking large areas in the environment has been shown to be a viable method for studying movement patterns in a broad range of insects. Immunomarking techniques using crude proteins (Jones *et al*. 2006, Hagler and Jones 2010,

Jones *et al*. 2011) are highly sensitive, relatively inexpensive, flexible, and appropriate for use in a wide range of applications. Insects can acquire the protein markers directly by being sprayed or indirectly by walking across a substrate with the protein residue. Insects can subsequently be captured by sticky traps and tested for the presence of the protein with an enzyme-linked immunosorbent assay (ELISA). I used immunomarkers to ask whether insects in celery systems interact with the margins and whether they move into the field from the margins. Specifically, I (1) measured the abundance and spatial distribution of arthropods in the fields and margins in Michigan commercial celery, (2) estimated the degree to which the arthropod community interacts with the margin, (3) assessed the movement of the arthropod community from the margin to the field, and (4) determined whether mean relative abundance correlates with positive mark percentage.

Materials and Methods

Study sites. In the 2013 and 2014 growing seasons, I selected three Michigan commercial celery farms based on large production volume, geographic separation, and grower cooperation. Farms were located in Allegan and Van Buren counties with a geographical separation ranging from 35.2 km to 72.2 km (mean distance: 57.1 km). Three fields from each farm were selected for study. Two fields on each farm were used for investigating the abundance and spatial distribution of arthropods. To maintain the independence and comparability of observations, I selected fields that had been planted at the same time, but were as far apart as possible. A third field with overgrown margin vegetation was selected for the mark-capture study. Over-grown margins were used because they come nearest to representing a refuge strip. In total, nine separate fields were used, six for abundance and distribution observations and three for the mark-capture study.

Mark-capture. In one field per farm, we established a sampling zone with four transects that were arranged perpendicular to the field edge and extended from the margins into the field. The sampling zone was defined as the middle 150 meters of the entire field length with transects evenly spaced at 50m intervals (Fig 3.1). Four fixed sampling positions were located along each transect at the following points: the margin, the field edge, 10m into the field, and 25m into the field for a total of sixteen sampling locations per field. A 76.2 x 1.3 cm galvanized pipe was hammered into the ground at each sampling position until the top edge was just above the canopy. The middle 250 m of each margin was sprayed until runoff with a solution of 10% albumin + 0.3 g/l of ethylenediamine tetra acetate (EDTA; ED4SS; Sigma-Aldrich) using a backpack sprayer with a three-nozzle boom at 30-40 psi. The top and underside of all foliage was sprayed to a depth of approximately one meter, bringing the total area of each margin sprayed to ~250 m^2. I placed yellow sticky traps (25.4 x 40.6 cm, Great Lakes IPM, Vestaburg, MI) at each of the sampling positions. Traps were removed from the field after 48-72 hours and transported

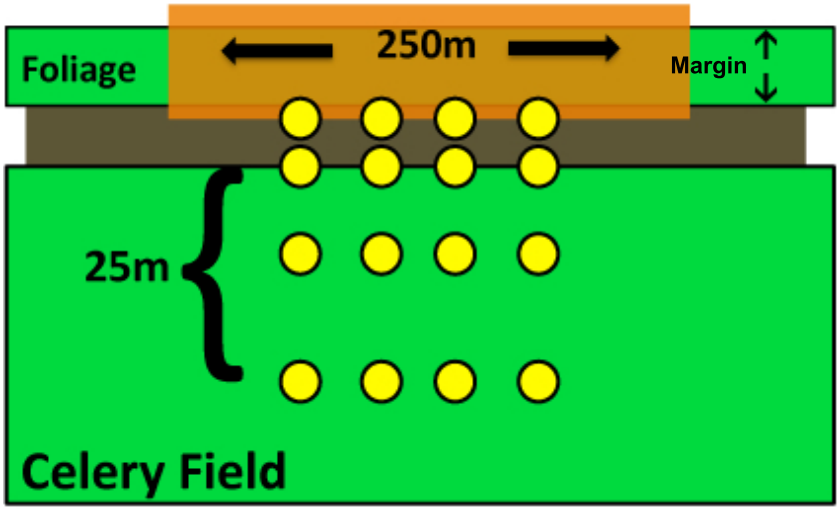

Figure 3.1. Mark-capture sampling design. Transects for yellow sticky traps were established in three commercial celery fields across three farms in southwest Michigan in July 2014. Yellow dots denote sampling locations. Orange rectangle denotes protein application area.

to the laboratory in a cooler. Individual insects were carefully removed from the sticky trap, each with a new wooden toothpick. Toothpicks were inserted into a 1.5 ml microcentrifuge tube and submerged in 1 ml solution of tris-buffered saline (TBS; 94158; Sigma-Aldrich) + 0.3 g/l EDTA. After 3 minutes, the insect and toothpick were removed and discarded. Samples were labeled and placed in a freezer (-20°C) to be tested in immunoassays for the presence of the protein at a later date.

I conducted an array of tests to check for the possibility of false positives and contamination by spray drift. One week prior to spraying, I collected leaf samples from four dominant plant species that were growing in the field margins on each farm to determine if the foliage possessed a protein that would trigger a false positive. Leaf samples were placed individually in 1-gallon plastic storage bags and taken to the laboratory for analysis. A single leaf disc, 7mm in diameter, was removed from each sample using a hollow punch and placed in a 1.5 ml tube containing 1ml of the extraction buffer with forceps. After 3 minutes, the sample was removed and discarded. The hollow punch, the forceps, and the cutting mat upon which the samples were placed were all sanitized with an 80% ethanol solution and wiped with clean Kimwipes (Kimberly-Clark, Roswell, GA) after each sample. In addition, I tested celery foliage both for the possibility of a false positive and for contamination from spraying the marker. Four leaf samples were taken from four randomly selected celery plants in the first row nearest the margin and placed in individual storage bags the week before spraying. Upon removal of the sticky traps at the end of the field experiment, four additional leaf samples were taken from the row nearest the sprayed margin (within the bounds of the spray area) and placed into individual plastic storage bags. Leaf discs and assay samples were prepared immediately after returning to the laboratory and in the same manner as previously described for the margin foliage. Finally, I

used a sweep net to collect representative samples of the insect community in the celery fields and margins of all three farms to determine if any species possessed a protein that would trigger a false positive. I selected a suitable range of taxa from this collection and acquired samples by submerging individuals in the extraction buffer as previously described. Samples in microcentrifuge tubes were labeled appropriately and stored in a freezer (-20°C) to be tested in immunoassays for the presence of the protein at a later date.

Immunoassays. Indirect ELISAs (Crowther 2001) were performed on all samples as described by Jones *et al*. (2006, 2011). The primary antibodies utilized in all immunoassays were for chicken egg albumin produced in rabbit (rabbit anti-chicken) (C6534; Sigma-Aldrich), whereas secondary antibodies were donkey anti-rabbit with peroxidase conjugate (31458; Thermo Scientific). The blocking buffer used in all assays was a solution of 0.3% Bovine Serum Albumin (BSA; B9433; Sigma-Aldrich) in phosphate-buffered saline (PBS; P4417; Sigma-Aldrich). As suggested by Jones *et al.* (2011), antibodies were mixed in a diluent buffer created from PBS and 1300 ppm Silwet L-77 for purposes of economy and assay optimization (Crowther 2001). Dilution ratios of 1:6000 for primary antibodies and 1:8000 for secondary antibodies were determined by the checkerboard titration process and used in all subsequent assays (Crowther 2001). All incubations were performed in an incubator oven (Lab-line Imperial III) set to 37°C. All buffered solutions were prepared with filtered and deionized water (Barnstead Nanopure II).

To test for the presence of the marker, 80 μl of each insect sample was placed in a separate well of a 96-well microplate (Nunc-Immuno; M0661; Sigma-Aldrich). A solution of 10% antigen in sample extraction buffer (TBS + EDTA) was used for a positive control, with just the extraction buffer used for negative control and blanks. Microplates were incubated for

120 minutes, after which, the contents were discarded. Wells were washed five times with 300 μl of PBS + 0.09% Triton X100 (PBST; X100; Sigma-Aldrich) followed by an addition of 300 μl of blocking buffer to every well. Microplates were then incubated for 60 minutes, after which the contents were discarded. The wells were washed two times with 300 μl of PBST and an 80 μl aliquot of properly diluted primary antibodies was placed into each well. The microplates were incubated for 30 minutes, the contents were subsequently discarded, and the plates washed five times with PBST. Secondary antibodies in 80 μl aliquots were added to each well and incubated for 120 minutes. The contents were discarded and the plates were washed three times with a solution of PBS + 2.3g/l sodium dodecyl sulfate (SDS; L4509; Sigma-Aldrich) followed by three washes with PBS. Once a chromogenic substrate (1-Step Ultra TMB; 34028; Thermo Scientific) in 80 μl aliquots was added to each well, plates were wrapped in aluminum foil and allowed to develop in the dark at 25°C. After 20 minutes, the reaction was stopped with the addition of 80 μl of 2N H_2SO_4 to each well. The optical density of each well was read with a plate reader (SpectraMax M5, Molecular Devices, California, USA) at a wavelength of 450 nm with 490 nm used as a reference standard. Wells with the extraction buffer (TBS + EDTA) were used as blanks to correct all readings. The values for optical density range from 0-4, with higher numbers associated with darker colors caused by higher concentrations of the antigen. I used the conservative threshold of 4 standard deviations above the mean optical density for negative control wells on a plate to determine whether a sample was positive for a mark (Jones *et al*. 2006, 2011).

Arthropod abundance patterns. To assess the relationship between relative margin abundance and margin usage (expressed as percent positive for marker), I sampled the celery fields with

yellow sticky traps placed at canopy level to acquire spatial abundance data. In each of the remaining six fields (see *Methods - Study sites*), I established three transects that were arranged perpendicular to and spatially equidistant along the field edge and extended from the margins into the field. Transect length was uniform and determined by the distance between the edge and the middle of the most narrow field. Four fixed sampling positions were located along each transect at the following points: the margin, the crop edge, 10m into the field, and 25m into the field for a total of twelve traps per field (Fig 2.3). I used non-baited 7.6 x 12.5 cm yellow sticky traps (Great Lakes IPM, Vestaburg, MI) placed at canopy level with wire loop hangers inserted into one end of 76.2 x 1.3 cm galvanized pipes. Traps were recovered after one week and arthropods of interest were counted and identified to the lowest possible taxonomic unit.

Statistical analysis. To determine if there were significant differences in the proportion of insects testing positive for the marker, I performed Fisher's Exact Test (FET) in R (R Core Team, 2014) using the number of positive marks and the number of negative marks. This test returns the exact probability of observing the data on the null hypothesis that the proportions are equal. Data were pooled across taxa to generate the overall proportion of the community that tested positive at each sampling position. I performed pair-wise comparisons between all sampling positions using the Holm-Bonferroni correction for family-wise error rate. Due to low numbers of positive marks, data for individual taxa at the margin and edge positions were combined into one proportion and compared to the combined data for the 10m and 25m positions. The resulting two categories represent insects that were collected in the immediate vicinity of the margins (within ~1m) and insects collected within the field interior (10-25m away). This comparison

serves as an indicator of propensity to move from the margin into the field. To maintain consistency, the overall community proportions were also analyzed in this manner.

I used R and *lme4* (Bates, Maechler, Bolker, Walker, Christensen, Singmann, Dai, and Grothendieck 2015) to perform a mixed-model logistic regression of the relationship between distance from the margin and the proportion of insects that tested positive. Distance was entered as the fixed-effect predictor, field was a random effect, and a two-vector object containing the number of positive and the number of negative marks served as the binomial response variable.

To determine if relative margin abundance can predict the degree of interaction with the margin (expressed as percent positive for marker), I used data from two different sources. Data from the concurrent six-field spatial abundance study was used to derive a predictor statistic and data from the three-field mark-capture component (percent positive) was used as the response variable. For the predictor statistic, I calculated the mean number of individuals captured per 7.6 x 12.5 cm yellow sticky trap at each sampling position across all six fields for taxa of interest. I then created a ratio of mean margin abundance (M_{margin}) to the average mean abundance of the other three sampling positions (M_{edge}, M_{10}, M_{25}), hereinafter referred to as the margin-field ratio (MF ratio) (3.1). I used R (R Core Team 2014) and a linear model (*lm*) to perform a simple linear regression of the relationship between the margin-field ratio and the overall percent marked positive for arthopods of interest. The margin-field ratio was entered as the fixed effect and the percent positive was used as the response variable. Regressions were performed on feeding functional groups (herbivores, predators, parasitoids) in addition to all of the groups combined.

$$\text{MF ratio} = \frac{M_{margin}}{(M_{edge}+M_{10}+M_{25})/3} \tag{3.1}$$

Results

Overview. I removed a total of 1606 arthropods across 44 different taxonomic groups from 48 yellow sticky traps and tested them for the presence of the protein marker. Of these arthropods, 147 (9.2%) tested positive for albumin (Table 3.1). Across taxonomic groups, the percentage of positive marks ranged from 0-38.5% (Table 3.1); at least one of the groups was significantly different (P=0.019, four-sample Fisher's Exact Test, FET). The proportion of positive marks was lowest at the field edge (6.5%, Table 3.1) with proportions 58%, 93%, and 19% greater at the margin, 10-meter, and 25-meter positions, respectively (Table 3.1). The difference in proportion between the edge and the 10m was the only pair-wise comparison with statistical significance (P=0.031, pair-wise FET, Holm-Bonferroni adjustment). The combined proportion of insects with a positive mark that were captured in the margin and edge was not significantly different from the combined proportion of protein-positive captures at the interior field locations (P=0.255, FET).

Among the 44 taxonomic groups I analyzed, 29 (65.9%) had at least one individual that tested positive for the marker (Table 3.1, Fig S10). Of these 29 groups, 19 different taxa (65.5%) had at least one individual testing positive at the 25m location and 23 taxa (79.3%) had at least one individual testing positive at either interior position (Table 3.1, Fig. S10). Despite significant differences for pair-wise comparisons, distance from the margin was not a significant predictor of the percentage of samples found positive for the marker (z=0.024, df=449, P=0.981, mixed-model logistic regression).

To determine whether relative margin abundance can predict the degree of interaction with the margins (as measured by percent positive for marker), I used all taxonomic groups from the mark-capture study in which there were 10 or more individuals tested. I then calculated a

margin-field abundance (MF) ratio (as described in *Methods* section) for these groups and eliminated those for which there were no individuals captured in the field (i.e. ratio is undefined), resulting in a total of 27 taxonomic groups suitable for evaluation. For reference, mean abundance (standardized for visual comparison purposes only) at all sampling positions for the 27 taxa are displayed in Fig. 3.2. Overall, the MF ratio was not a significant predictor of the proportion of individuals that tested positive for the protein marker; the two parameters were not correlated (R^2=0.006, F=0.161, df=1, 25, P=0.692, Fig 3.3). For herbivores, the MF ratio was not a significant predictor of the proportion of individuals that tested positive for the protein marker; the two parameters were not correlated (R^2=0.048, F=0.698, df=1, 14, P=0.417, Fig 3.3). For predators, the MF ratio was not a significant predictor of the proportion of individuals that tested positive for the protein marker; the two parameters were not correlated (R^2=0.198, F=1.23, df=1, 5, P=0.318, Fig 3.3). For parasitoids, the MF ratio was a significant predictor of the proportion of individuals that tested positive for the protein marker; the two parameters were correlated (R^2=0.9304, F=26.73, df=1, 2, P=0.035, Fig 3.3). However, one regression point in the parasitoid analysis was highly influential. Once this point was removed from the analysis, the correlation was no longer significant (R^2=0.051, F=0.053, df=1, 2, P=0.856).

Because proportions differed across sampling position and taxonomic groups, individual taxa of interest were analyzed separately:

Aster leafhopper. I recovered and tested a total of 41 aster leafhoppers, of which 6 (14.6%) tested positive for the marker (Table 3.1). The proportion of positive marks was lowest at the edge position (7.1%, Table 3.1) with proportions at the margin, 10-meter, and 25-meter positions greater by factors of 1.625, 1, and 2.5, respectively. When combined, the proportion of protein-

positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.651, FET). Likewise, distance from the margin did not significantly influence the proportion of samples positive for the marker (z= 0.517, df=9, P=0.655, mixed-model logistic regression).

Potato leafhopper. I recovered and tested a total of 156 potato leafhoppers, of which 8 (5.1%) tested positive for the marker (Table 3.1). The proportion of positive marks was lowest at the 25-meter position (0%, Table 3.1). Proportions at the margin and 10-meter positions were greater than the edge position by factors of 1.5 and 3.7, respectively (Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.492, FET). Distance from the margin was not a significant predictor of the proportion of samples testing positive for the marker (z= -0.697, df=9, P=0.268, mixed-model logistic regression).

Tarnished plant bug. I recovered and tested a total of 52 tarnished plant bugs, of which 20 (38.5%) tested positive for the marker (Table 3.1); this was the highest percentage of any group. Proportions at the margin and edge positions were nearly the same (48.0 and 50.0%) and also ≈50.0% and ≈450.0% greater than the proportion positive at the 10-meter and 25-meter positions. When combined, the proportion of protein-positive insects captured within 1m of the margins was significantly different from the proportion captured at the interior field positions (P=0.038, FET). When modeled, distance was also found to significantly influence the proportion of samples positive for the marker (z=-2.181, df=9, P=0.029, mixed-model logistic regression).

Syrphidae. I recovered and tested a total of 25 syrphid flies, of which 7 (28.0%) tested positive for the marker (Table 3.1); this was the highest percentage of any natural enemy group. The proportion of positive marks was highest in the margins (57.1%); the other positions were lower (average 16.7%) but similar to each other (Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=1.000, FET). Distance from the margin was not a significant predictor of the proportion of positive marks (z=-0.738, df=9, P=0.461, mixed-model logistic regression).

***Coleomegilla maculata*.** I recovered and tested a total of 15 *Coleomegilla maculata* (CMAC) specimens, of which 4 (26.7%) tested positive for the marker (Table 3.1). This was the only lady beetle species to test positive for the marker and was also the natural enemy group with the 2nd highest percentage. Positive marks were found only at the interior sampling locations, with the proportion at the 10-meter location (2 positive/3 individuals) larger than that of the 25-meter location (2/6) by a factor of 2 (Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.103, FET). Distance from the margin was not a significant predictor of the proportion of positive marks (z=1.11, df=9, P=0.267).

Chamaemyiidae. I recovered and tested a total of 50 chamaemyiid flies, of which 7 (14.0%) tested positive for the marker (Table 3.1); this was the third highest percentage among natural enemy taxa. The proportion of positive marks was lowest in the margins (0%, Table 3.1). Proportions at the other three sampling locations were similar to each other, differing largely by

the total number of tested specimen as opposed to the number of positive marks (2, 3, and 2 positive specimens at the edge, 10-meter, and 25-meter positions, respectively; Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.225, FET) and distance from the margin did not significantly influence the proportion of positive marks (z=1.152, df=9, P=0.337).

Braconidae. I recovered and tested a total of 46 braconid wasps, of which 4 (8.7%) tested positive for the marker (Table 3.1); this was the highest percentage among parasitoid groups. All four of the positive marks were found on insects recovered from the margins (Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.313, FET). Distance was not a significant predictor of proportion positive (z=-0.002, df=9, P=0.998; simple logistic regression).

Mymaridae. I recovered and tested a total of 76 mymarid wasps, of which 5 (6.6%) tested positive for the marker (Table 3.1). The proportion of positive marks was highest at the 10-meter position (18.2%, Table 3.1). However, the proportions at all four sampling locations were similar to each other, differing largely by the total number of tested specimen as opposed to the actual number of positive marks (1, 1, 2, 1 positive marks at margin, edge, 10-meter, 25-meter positions, respectively; Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.378, FET). Distance from the margin did not significantly

influence the proportion of positive marks (z=0.316, df=9, P=0.752, mixed-model logistic regression).

Chalcidoidea. I recovered and tested a total of 114 chalcidoid wasps, of which 9 (7.9%) tested positive for the marker (Table 3.1). The proportion of positive marks was highest at the 10-meter location (14.3%, Table 3.1). However, the proportions at all four sampling locations were similar to each other, differing largely by the total number of tested specimen as opposed to the actual number of positive marks (2, 2, 3, 2 positive marks at margin, edge, 10-meter, 25-meter positions, respectively; Table 3.1). When combined, the proportion of protein-positive insects captured within 1m of the margins was not significantly different from the proportion captured at the interior field positions (P=0.314, FET). Distance from the margin did not significantly influence the proportion of positive marks (z=0.565, df=9, P=0.572).

Controls.

***Plant tissue*.** I sampled leaf tissue from a total of 19 different plant taxa, including the celery field, one week prior to the protein application; all samples tested negative for the presence of the protein marker (Table S2). Eight leaf samples from the first row of celery in every mark-capture field were acquired at the end of the experiment to assess possible contamination. At least one celery sample from each farm tested positive for the presence of the protein marker, indicating contamination at all three study locations. The percentage of post-application celery samples testing positive for the presence of the marker ranged from 12.5-25.0% percent across farms for a mean contamination percentage of 16.7% (Table S2). However, the proportion of contamination was not found to significantly influence the proportion of marked arthropods

across farms (t=-1.018, df=1, P=0.494). Samples from the sticky traps deployed in the mark-capture experiment were also tested to check for possible analogous protein cross-contamination as well as contamination from field activities; all samples tested negative for the protein (Table S2). Leaf samples from post-application margin foliage were acquired to confirm the presence of the protein residue; all samples tested positive for the presence of the protein marker (Table S2).

Insect negative control. Similar to the margin and celery foliage, insects from all three farms were collected with sweep nets one week prior to protein application to check for possible cross-contamination from analogous proteins. A total of 140 insects in 26 different taxonomic groups were collected; all samples tested negative for the presence of the protein (Table S3).

Table 3.1. The number of arthropods (n) recovered from yellow sticky traps deployed at four sampling positions across three celery farms in southwest Michigan. Percentage (%) indicates the proportion of taxa testing positive for the presence of chicken egg protein marker; hash sign (#) indicates the number of positive marks.

	Margin			Edge			10m			25m			Total		
Taxon	**n**	**%**	**(#)**	**n**	**%**	**(#)**	**n**	**%**	**(#)**	**n**	**%**	**(#)**	**n**	**%**	**(#)**
HEMIPTERA															
Macrosteles quadrilineatus	16	18.8	(3)	14	7.1	(1)	7	14.3	(1)	4	25.0	(1)	41	14.6	(6)
Macrosteles spp. (other)	2	0.0	(0)	2	0.0	(0)	0	0.0	(0)	1	0.0	(0)	5	0.0	(0)
Empoasca fabae	45	4.4	(2)	34	2.9	(1)	36	13.9	(5)	41	0.0	(0)	156	5.1	(8)
Cicadellidae (other)	12	8.3	(1)	10	30.0	(3)	8	12.5	(1)	7	0.0	(0)	37	13.5	(5)
Cercopidae	1	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	100.0	(1)	2	50.0	(1)
Aphididae	32	0.0	(0)	46	4.3	(2)	35	14.3	(5)	29	3.4	(1)	142	5.6	(8)
Lygus lineolaris	25	48.0	(12)	10	50.0	(5)	6	33.3	(2)	11	9.1	(1)	52	38.5	(20)
Lygus spp. (other)	2	50.0	(1)	10	0.0	(0)	22	4.5	(1)	39	7.7	(1)	73	6.8	(5)
Miridae	5	60.0	(3)	8	0.0	(0)	2	50.0	(1)	7	28.6	(2)	22	27.3	(6)
Psyllidae	13	0.0	(0)	4	0.0	(0)	5	20.0	(1)	2	50.0	(1)	24	8.3	(2)
Membracidae	20	40.0	(8)	4	50.0	(2)	3	33.3	(1)	3	0.0	(0)	30	36.7	(11)
Cydnidae	1	100.0	(1)	6	16.7	(1)	8	12.5	(1)	2	50.0	(1)	17	23.5	(4)
Aleyrodidae	8	0.0	(0)	12	0.0	(0)	6	0.0	(0)	9	0.0	(0)	35	0.0	(0)
Anthocoridae	62	1.6	(1)	50	10.0	(5)	20	15.0	(3)	18	5.6	(1)	150	6.7	(10)
CHRYSOPIDAE	2	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	0.0	(0)	3	0.0	(0)
ARANAE	27	7.4	(2)	38	5.3	(2)	26	7.7	(2)	14	0.0	(0)	105	5.7	(6)
COCCINELLIDAE															
Coccinella septempunctata	0	0.0	(0)	0	0.0	(0)	1	0.0	(0)	1	0.0	(0)	2	0.0	(0)
Coleomegilla maculata	1	0.0	(0)	5	0.0	(0)	3	66.7	(2)	6	33.3	(2)	15	26.7	(4)
Harmonia axyridis	4	0.0	(0)	3	0.0	(0)	2	0.0	(0)	1	0.0	(0)	10	0.0	(0)
Propylea quatuordecimpunctata	1	0.0	(0)	3	0.0	(0)	0	0.0	(0)	1	0.0	(0)	5	0.0	(0)
Symnus spp.	0	0.0	(0)	2	0.0	(0)	1	0.0	(0)	2	0.0	(0)	5	0.0	(0)
CHRYSOMELIDAE															
Phyllotreta spp.	5	20.0	(1)	3	0.0	(0)	3	0.0	(0)	0	0.0	(0)	11	9.1	(1)
Other	22	0.0	(0)	27	3.7	(1)	8	0.0	(0)	9	0.0	(0)	66	1.5	(1)
COLEOPTERA (Other)															
Cantharidae	0	0.0	(0)	2	0.0	(0)	2	0.0	(0)	1	0.0	(0)	5	0.0	(0)
Mycetophagidae	1	0.0	(0)	0	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	0.0	(0)
Staphylinidae	9	0.0	(0)	6	0.0	(0)	8	12.5	(1)	6	16.7	(1)	29	6.9	(2)
Curculionidae	8	25.0	(2)	6	0.0	(0)	5	0.0	(0)	0	0.0	(0)	19	10.5	(2)
ICHNEUMONOIDEA															
Braconidae	17	23.5	(4)	16	0.0	(0)	8	0.0	(0)	5	0.0	(0)	46	8.7	(4)
Aphidiidnae	1	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	0.0	(0)	2	0.0	(0)
Ichneumonidae	1	0.0	(0)	3	33.3	(1)	1	0.0	(0)	0	0.0	(0)	5	20.0	(1)
Other	1	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	100.0	(1)	2	50.0	(1)
CHALCIDOIDEA															
Mymaridae	29	3.4	(1)	17	5.9	(1)	11	18.2	(2)	19	5.3	(1)	76	6.6	(5)
Trichogrammatidae	4	0.0	(0)	3	0.0	(0)	1	0.0	(0)	4	0.0	(0)	12	0.0	(0)
Other	33	6.1	(2)	36	5.6	(2)	21	14.3	(3)	24	8.3	(2)	114	7.9	(9)
HYMENOPERA (Other)															
Vespidae	0	0.0	(0)	1	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	0.0	(0)
Formicidae	0	0.0	(0)	2	0.0	(0)	0	0.0	(0)	0	0.0	(0)	2	0.0	(0)
DIPTERA															
Chamaemyiidae	12	0.0	(0)	15	13.3	(2)	13	23.1	(3)	10	20.0	(2)	50	14.0	(7)
Syrphidae	7	57.1	(4)	9	11.1	(1)	3	33.3	(1)	6	16.7	(1)	25	28.0	(7)
THYSANOPTERA															
Thripidae	37	2.7	(1)	37	0.0	(0)	39	10.3	(4)	34	5.9	(2)	147	4.8	(7)
Aeolothripidae	11	0.0	(0)	11	0.0	(0)	11	9.1	(1)	10	10.0	(1)	43	4.7	(2)
PSCOPTERA	6	16.7	(1)	4	0.0	(0)	1	0.0	(0)	3	0.0	(0)	14	7.1	(1)
ACRIDIDAE	1	0.0	(0)	0	0.0	(0)	0	0.0	(0)	0	0.0	(0)	1	0.0	(0)
LEPIDOPTERA	1	0.0	(0)	1	0.0	(0)	0	0.0	(0)	2	50.0	(1)	4	25.0	(1)
TOTAL	**485**	**10.3**	**(50)**	**460**	**6.5**	**(30)**	**326**	**12.6**	**(41)**	**335**	**7.8**	**(26)**	**1606**	**9.2**	**(147)**

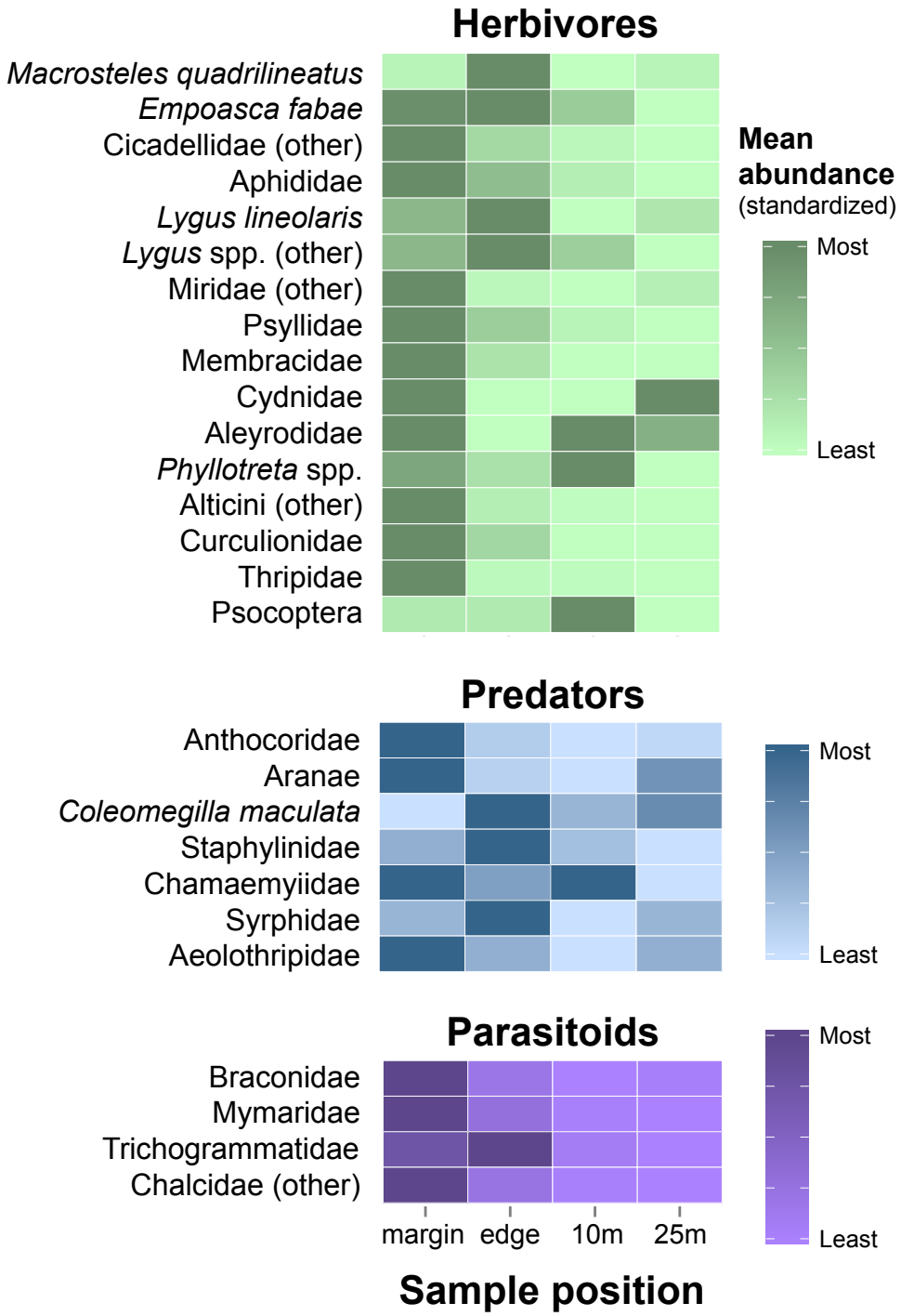

Figure 3.2. Mean abundance of arthropods at four different sampling positions from data collected with yellow sticky traps in six fields across three different celery farms in southwest Michigan during the first week of July 2014. Data are standardized on a scale ranging from 0-1 to enable comparisons across taxa.

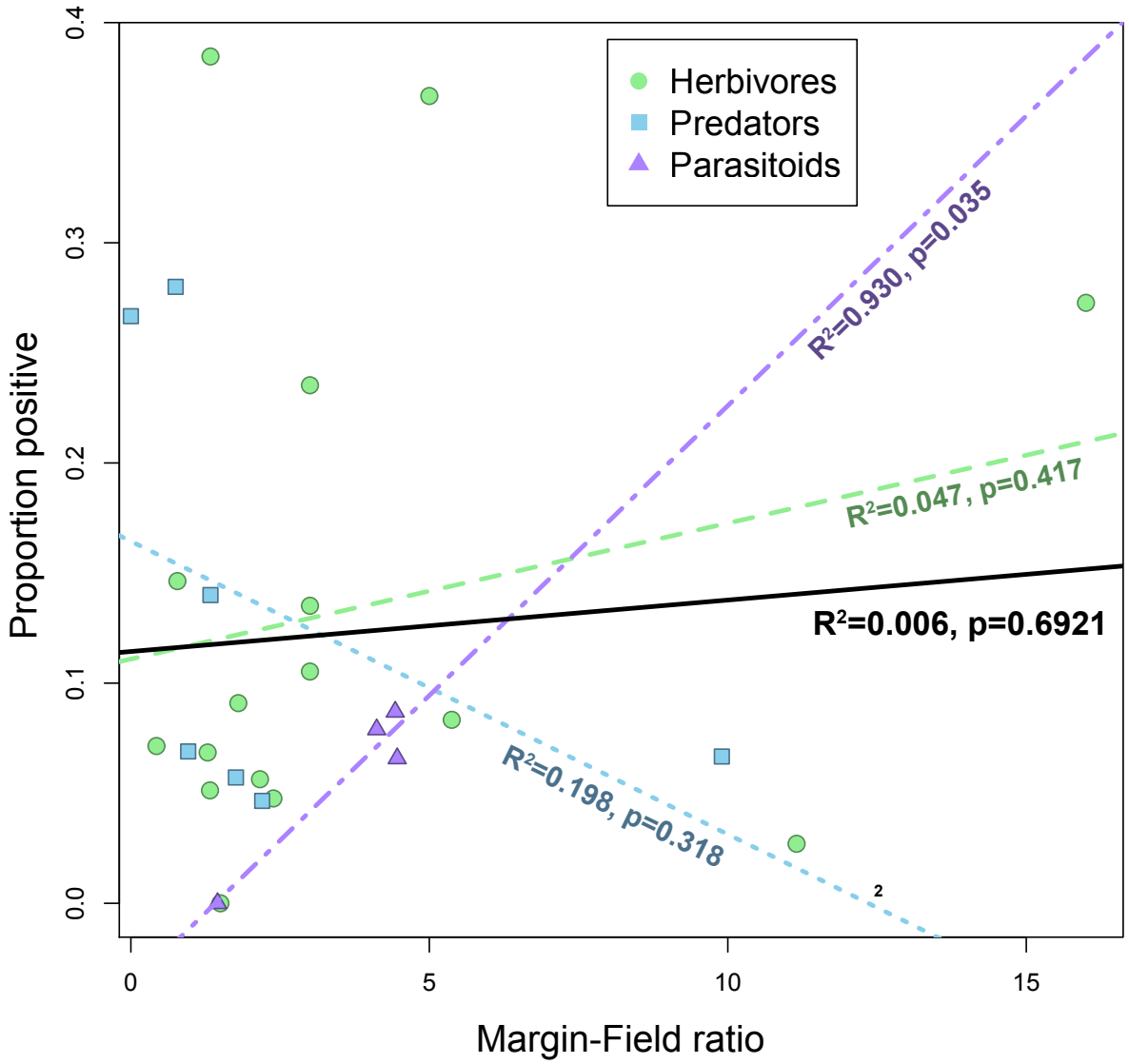

Figure 3.3. The relationship between the Margin-Field ratio (MF) and the proportion of individuals testing positive for the presence of the chicken egg protein marker. The MF ratio is the abundance of arthropods caught in the margin relative to those caught in the celery field (please see *Methods* section). Regression points and lines were plotted with different symbols and colors according to feeding functional group. The black regression line is the result of all points in a singular analysis.

Discussion

In my field study, I investigated the movement and spatial distribution of canopy arthropods in Michigan celery fields. I measured mean abundance at various distances into the field, quantified movement patterns, and assessed the degree to which key groups interact with the margins. Over 65% of the groups analyzed for the presence of the marker had at least one individual test positive and almost 80% of those groups tested positive at either interior field position. This suggests that the majority of the canopy arthropod community in celery systems interact with the margins to some extent and that these groups move from the margins into the field. In terms of the whole community, distance did not significantly influence the proportion of insects testing positive for the marker. Likewise, there was no significant difference between the proportion of protein-positive insects captured near the margins and those captured at the interior positions. These results indicate that the typical dispersal distance by any given arthropod is greater than 25 meters and that re-colonization of a field after a pesticide application occurs rapidly. It also suggests that, in general, the hard edges of the crop-soil-margin interface do not seem to hinder the canopy community from moving between margin and field, although there may be specific groups for which it does (e.g. TPB, syrphids). Most importantly, however, it shows that natural enemy groups would be able to respond to prey aggregation at the innermost part of a celery field.

The percentage of individuals within taxonomic groups that tested positive for the presence of the marker ranged from 0-38.5% with an overall average of 9.2%. The distribution of proportions positive for the marker across the 27 taxa in the analysis was skewed low; only ten groups had proportions higher than the average. Because the percentages varied widely, I analyzed several key arthropod groups separately. While this method strengthened my ability to

assess differences in proportions across taxa, I acknowledge that the low number of positive marks imposes limitations on conclusions made about the movement patterns of specific athropod groups. Therefore, I focus primarily on overall percentages, proximity to the margin, and the furthest distance travelled.

The proportion of tarnished plant bugs (38.5%) and aster leafhoppers (14.5%) testing positive for the protein were the highest among key pests and well above the community average. Collectively, 85% of the protein-positive tarnished plant bugs and 66% of the protein-positive aster leafhoppers were captured within 1 meter of the margin, which suggests a high propensity to stay near the margin when moving about. For comparison, 90.9% of protein-marked treehoppers, *Acutalis* spp. (Hemiptera: Membracidae), which are common in celery margins due to host plant associations with abundant ragweed species (*Ambrosia* spp.), were captured within 1 meter of the sprayed area (Table 3.1; Fig. S10; J. Jubenville, pers. obs.). I speculate that the limited movement pattern in TPB and ALH could be indicative of habitat preference. Although they are both highly polyphagous species, if the margins serve as refuge and the plants in the margins are a consistent non-toxic food resource, then plant host habituation may explain this movement pattern (e.g. Bancroft 2005). Nevertheless, positive marks for both the TPB and ALH were found at all sampling positions within the celery field. This indicates that some proportion move into the field interior and suggests that they can easily forage anywhere within the field from the margins.

Aphids, thrips, and potato leafhoppers were well below the average percent positive, suggesting a relatively low degree of interaction with border areas. These groups are usually considered part of the aerial plankton pool and may only interact with the margins in this system on an incidental basis. Together, 25%, 14.3%, and 37.5% of protein-positive aphids, thrips, and

PLH, respectively, were captured at the margin and edge positions (within ~1 meter of the sprayed areas), suggesting that they are not as inclined to stay near the margins as TPB and ALH. Interestingly, potato leafhoppers had one of the lowest percentages (5.1%) of herbivores in the study despite being the most abundant cicadellid species during the two seasons (CHAPTER 2, Table S1). Potato leafhopper ecology is much like that of the aster leafhopper in that a small proportion of the population overwinters within Michigan, but the majority migrate on the wind from southern states. Potato leafhoppers, like aster leafhoppers, are also agile flyers but clearly interact with the margins to a lesser extent (5.1 versus 14.5% positive).

Among predators, only three taxonomic groups had protein-positive percentages higher than the study average: the pink spotted lady beetle, CMAC (26.7%), and two dipteran families, Syrphidae (28.0%) and Chamaemyiidae (14.0%). All of the protein positive CMAC specimens were captured at the interior field positions, suggesting little propensity to stay near the margins. *Coleomegilla maculata* is different than the other lady beetle species in this system. Not only is it far more abundant than others (CHAPTER 2, Table S1), but it is also the only coccinellid that tested positive for the presence of the marker. In addition to insect prey, this lady beetle species is known to feed on floral resources and fungal spores (Webber and Lundgren 2009), which are likely to be far more abundant in the margins than the field due to weekly fungicide use in the field. Flowers are also occasionally present within the margins and usually found on faster-developing species such as smartweed (*Polygnum* spp.) and field bindweed (*Convolvulus arvensis*). Because of this, CMAC may frequently visit celery margins to forage for prey, pollen, and spores, but the margins are likely one of many habitats it may visit on any given day.

With the dipteran predators, 71% of the marked syrphids and 28.5% of the marked chamaemyiids were captured within 1 meter of the margin, indicating that syrphids have a higher

propensity to stay near the margins. Syrphid flies feed on nectar as adults and were consistently observed on smartweed flowers growing in field borders (J. Jubenville, pers. obs.). Floral resources are known to enhance local syrphid populations in agricultural landscapes (Cowgill *et al.* 1993, Blaauw & Isaacs 2012) and celery margins can, at times, provide a combination of flowers, refuge, and oviposition sites (i.e. nearby prey for offspring). As such, it seems likely that syrphids use these margins as habitat when conditions are favorable. Chamaemyiids seem to be rangy fliers (J. Jubenville, pers. obs.) and likely use this vagility to forage within a variety of habitats. As with CMAC, chamaemyiids are frequent visitors to margins, but their overall association is moderate compared to other groups. Both dipteran groups had positive marks at the furthest location from the sprayed areas, suggesting that they will forage throughout the field after interacting with the margin.

Among the parasitoids, Braconidae (8.7%), Mymaridae (6.6%), Trichogrammatidae (0.0%), and other Chalcidoidea (7.9%) scored near or below the community average of 9.2%. Despite these numbers, 100%, 40%, and 44% of the protein-positive braconid, mymarid, and chalcioid wasps, respectfully, were captured within 1 meter of the margin. This indicates that the degree to which the prominent parasitoid groups interact with the margins is highly variable and may also be influenced by other factors (e.g. host availability). Positive marks for mymarid and chalcidoid wasps were found at all sampling locations, indicating that they will move throughout the field after interacting with the margin.

In the regression analysis, the points representing Mymaridae, Chalcidoidea, and Braconidae were clustered closely together (Fig. 3.3), while the point representing the Trichogrammatidae (0% positive) was located well outside this cluster and near the origin. When analyzed, the regression shows a highly significant positive relationship between the MF ratio

and the percent positive for parasitoids (R^2=0.9304, F=26.73, df=1, 2, P=0.035, Fig 3.3). However, when the Trichogrammatidae are removed from the analysis, thereby reducing it to a regression of three points, the correlation is no longer significant (R^2=0.051, F=0.053, df=1, 2, P=0.856). Caution should therefore be taken when forming conclusions based on this result.

The majority of specimens in every group tested negative for the presence of the marker. My interpretation of these results is that it is more likely that the majority of insects found within the celery fields come from sources other than the margins (but see *False negatives and false positives* and *Marking efficiency*). From an ecological standpoint, in order for margins to function as a source of arthropods, the rate of emigration would need to exceed the rate of immigration as well as the birth rate exceeding the death rate. Although this is something that I did not directly measure, the fact that margins are subject to intense ecological disturbance on a monthly basis (mowing, Fig 1.3) makes this an unlikely prospect for all but those species with the highest reproductive rates (e.g. aphids). Margins probably function as a refuge most weeks of the season and so abundance would be expected to be higher in these areas. As I have shown, however, a margin-centric pattern does not seem to be a reliable predictor of overall habitat use (Fig 3.3).

False negatives and false positives. The discovery of positive marks in this study is directly related to the threshold value for optical density. The OD of any particular sample must exceed the average OD of the negative control wells on the same plate by four standard deviations in order for it to be considered positive for the presence of the protein. This is a conservative threshold established by Jones *et al*. (2006) and is used in subsequent studies by Jones, Hagler, and others (e.g. Boina *et al.* 2009, Horton *et al*. 2009, Hagler and Jones 2010, Peck *et al*. 2014).

The cost of such a conservative approach is an inherent increase in false negatives. In their studies, Jones and Hagler were more interested in whether arthropods were moving from one location to another as well as the distance that a particular taxon moved from the sprayed location. They took care in making generalizations about how much any particular arthropod group utilized the sprayed areas. Likewise, they were also careful in how they compared the percent positive among taxa.

The question of where to set the threshold is comparable to the question of where we set our alpha value when performing statistical analyses. Using a small alpha increases the risk of not detecting a significant effect (false-negative) when one is actually present, whereas using a larger alpha increases the risk of declaring a significant effect (false-positive) when, in reality, one does not exist. This translates to my study in the following manner: if I increase the possibility of false negatives (higher OD threshold), then I risk underestimating the degree to which insects use the margins. If I increase the possibility of false positives (lower OD threshold), then I not only risk overestimating how much arthropods use the margins, but I also risk over-estimating their movement patterns as well. This is of particular importance when considering the question of whether natural enemies will move out into the center of the field to prey upon pests. In this study, I prefer the conventional conservative approach. This means that I may be underestimating the movement patterns and the degree to which any particular taxon interacts with the margins.

Marking efficiency. Another possible caveat is that different species may acquire positive marks with different efficiency. Hagler and Jones (2010) showed that it does not take long for a broad range of taxa to acquire positive marks from residual chicken egg protein on leaf tissue. In this

study they introduced unmarked arthropod assemblages acquired with sweep nets to field cages containing cotton plants previously sprayed with chicken egg whites. Subsequent sampling showed a high percentage of positive marks after one day and up to eleven thereafter. Overall percentages for the first four days after spraying ranged from 70% for Hymenoptera (mostly ants) to 96% for Coleoptera (many species). More relevant to my study is that 91% of Heteropterans tested positive after four days. These percentages indicate two important things: 1) most taxa will readily acquire residual egg protein in a field study under two weeks in duration (assuming no rain), and 2) there is likely a difference in the rate in which taxa acquire the marker. Furthermore, tarnished plant bugs, the group with the highest percentage in my study, are part of a group (Heteroptera) that demonstrated high marker acquisition efficiency in the Hagler and Jones (2010) study. Therefore, it is likely that I am underestimating the degree to which taxa interact with the margins, but the difference may be minimal.

Contamination. During the protein application process, the spray boom was pointed in the opposite direction of the field at all times. Nevertheless, at least one leaf sample taken from the first row of celery on each farm at the end of the experiment tested positive for the protein maker (Table S2). This means that insects could acquire the protein mark from walking on some of the celery foliage. This result is not surprising given that the first celery row is ~1m from the margin foliage and highlights two important points: ELISA assays are highly sensitive and margin foliage coverage was probably good. When interpreting the results of this study, it should be noted that the contamination in the field could result in an overestimation of margin usage and movement patterns. That being said, the amount of margin foliage covered in egg whites greatly

exceeded the amount that may have drifted into the field. Insects were far more likely to acquire marks from the margin than anywhere else.

Summary and Application. Understanding the sources of insects, their movement patterns, and how they utilize key areas in agricultural systems can have a positive impact on crop production. This is particularly important in the case of plant disease vectors where simple management changes may have a profound effect on local disease ecology (e.g. Boina et al. 2009). Knowledge of aggregation tendencies can be used to successfully reduce the frequency and impact of pest management actions in some crops by implementing tactics such as targeted spraying (e.g. Morrison and Szendrei 2013) and local habitat manipulation (e.g. Swezey et al. 2007, 2013).

The results of this study reveal differences in how various arthropod groups interact with the margins in Michigan celery systems. Variation in mark percentage, as well as the spatial distribution of the marks, shows that some groups utilize the margins more than others and these groups are comprised of both key pests and natural enemies. A useful application of this information is to predict how these groups might respond to alternative margin management strategies. Any systematic change in the way growers manage their margins would likely affect these groups to a greater degree than the other groups in the study. For instance, suppose we adopt a conservative approach, retain the current floral composition (mostly common agricultural weeds and grasses), and allow the margins to grow throughout the year. We could expect all of these groups to benefit from the habitat enhancement, but perhaps most conspicuously, tarnished plant bugs. A situation such as this could result in a dramatic increase in pest pressure, especially if pest control within the margin is not equally enhanced by the increase in stability.

A more productive approach may be to replace much of the current flora with a select mixture of flowering perennials. Syrphids, coccinellids, and parasitoids have all been found to exploit floral resources on the fringes of agricultural fields and subsequently disperse into the field. For example, Freeman Long *et al*. (1998) sprayed rubidium (Rb) on flowering strips and found Rb-labeled natural enemies as far as 75m into an orchard. Similarly, Nicholls *et al*. (2001) found that the presence of a flowering plant corridor enhanced natural enemy colonization of an adjacent vineyard. Most pertinently, Nicholls *et al.* (2001) noted that the influence of the flowering corridor was limited by natural enemy dispersal distance. In celery systems, where fields are often narrow and the edge-to-area ratio is high, dispersal to the center of the field from the margins is not likely to be a limiting factor in colonization success. The prospect of strengthening pest populations with this strategy is a concern (e.g. Winkler *et al*. 2009, 2010). However, previous research in southwest Michigan has shown that a thoughtfully designed mixture of flowering perennials can result in greater abundance of key natural enemy groups without a significant increase in herbivores. Blaauw and Isaacs (2012) found that cicadellid abundance declined dramatically and mirid abundance increased moderately with the addition of flowering perennials. Most notably, they documented an increase in pest control (aphids) on sentinel plants, but only when flowers were present. This speaks to the influence that floral resources may have on pest regulation in managed environments.

Conserving margins for beneficial insects in Michigan celery may be a relatively easy way to integrate an additional pest control strategy into these busy commercial systems. When combined with diligent scouting and economic thresholds, successful implementation of this strategy could provide growers with substantial economic benefits and reduce the environmental impact of intensive agricultural practices. Future research on this subject should consider how

habitat enhancement might affect key pest populations (e.g. Wackers 2001, Winkler *et al*. 2010) as well as the likelihood of pesticide drift into conservation areas. Additional work to establish economic thresholds for key pests would also be highly beneficial.

CHAPTER 4:

Conclusions and future research

There were two primary objectives of this thesis: 1) quantify spatiotemporal abundance patterns of arthropods in and around celery fields and 2) evaluate the likelihood of field margins as a source of insects in the crop. I proceed to achieve these objectives with a combination of inferential observation and direct measurement. In chapter two, I analyzed the spatial and temporal abundance patterns of a broad range of arthropods across the season. Given the narrow field profile with a short distance to the middle, a consistent edge-centric colonization pattern could signify that margins are a source for any particular group. On the other hand, I would expect a high-dispersal group interacting with the margins on an incidental basis to be evenly distributed (on average) across the field. In chapter three, I implement a mark-capture experiment to assess margin usage across a broad range of taxa. Although this is a far more direct method of answering my question, it is not without its own set of implications. I inferred, generally, that if a species was associated with the margin then it was more likely to have a relatively high percentage of marked individuals and that the majority of these marked individuals would be recovered in close proximity to the margin. When combined with the furthest distance a marked specimen is recovered, we can predict which species would be most likely to respond to margin enhancements and how that might affect the crop.

Land use within the modern agricultural landscape falls along a continuum of habitat stability, with areas of intense disturbance on one end and near-natural areas at the other. At the farm scale, crop fields are ephemeral habitats that bear frequent and intense disturbance while border areas often managed less frequently and with varying levels of intensity. Pest

management practices often cause arthropod extinction within the field, but border areas are not usually managed in this way. The inequality in disturbance between adjacent areas may result in a source-sink dynamic with arthropods from border habitats re-colonizing the suddenly unoccupied field. Whether this is considered a favorable circumstance depends on the degree to which pest species utilize these areas. Nevertheless, because local abundance can be influenced by factors at the landscape scale (Tscharntke 2005a), it should not be assumed that margins are the primary source of any group of insects found within the field. Understanding the origin of beneficial and pestiferous insects within a production system is fundamental to selecting the most suitable management practice. Chapter two characterizes the abundance and distribution patterns of the canopy arthropods based on the results of yellow sticky trap sampling at different distances into the field. In general, groups were either: 1) evenly distributed across all sampling locations, 2) most or least abundant in the margins, but evenly distributed throughout the field, or 3) most abundant at the margins/field edge and decreasing in abundance with greater distance into the field. I hypothesized that groups fitting into the last two categories are those that might interact with the margins to a higher degree and may therefore benefit from habitat enhancement in these areas. Among these groups are historically important pests as well as natural enemies and so their relationship with the margin needed to be quantified in a more direct manner before margin enhancements could be considered.

Celery systems are often comprised of groups of several long narrow fields separated lengthwise by drainage ditches (Fig 1.2). The fields are narrow enough that recolonization should occur rapidly. Margins and ditch banks are the nearest potential source of arthropods and growers manage them with this in mind; practices such as mowing and herbicide application are common. The degree to which any arthropod group used the margins, however, was not

established and growers managed them under the assumption that pestiferous herbivores would use them as habitat. Border habitats in other systems have been manipulated to encourage natural enemy populations through the addition of perennial floral resources. These types of modifications are intended to attract predators and parasitoids currently present within the landscape with the expectation that, once there, they will disperse within the field to provide natural pest control. Research has shown this strategy to work in some situations (Bianchi *et al*. 2006) and may be an employable strategy in Michigan celery systems. Many celery fields are narrow, with their centers approximately 25 meters from the edge. Conceptually, such narrow fields should be quickly re-colonized by mobile arthropods once the toxicity of pesticide residues begins to fade. In chapter three, I examined the degree to which the arthropod community interacts with the margins and how far they move out into the field. Margins were sprayed with a crude protein marker that would not normally be found in celery fields (i.e. chicken egg albumin). Arthropods acquired the marker directly by being sprayed or indirectly from walking on residue-covered foliage. We can use the results of this experiment in several ways: we can quantify how far the insects move into the field after interacting with the margins, we can estimate the degree to which the insects interact with the margins, and we can ascertain which groups have a propensity to stay near the margins. Over 90% of specimens tested negative for the protein, although the majority (65.9%) of groups had at least one positive mark. This suggests that most groups do interact with the margins, but only to a minor extent. Therefore, it does not appear that margins, as they are currently managed, serve as source of insects that are found in the celery field. I also assessed whether margin abundance (relative to field abundance, MF ratio) could predict margin usage (measured as overall percent positive) and found that there was no systematic relationship between the two. This was particularly important when

considering the spatiotemporal data for parasitoids, which provided clear margin-centric patterns (Fig. 2.7).

From the mark-capture results, we can see that some groups utilize the margins more than others and these groups are comprised of both key pests and natural enemies. If margins were left to grow in their current state, I would expect tarnished plant bug and syrphid fly numbers to increase along with Chamaemyiidae and *Coleomegilla maculata* numbers to a lesser extent. Importantly, all of these groups forage throughout the field while interacting with the margins. Perennial flowering strips could differentially benefit natural enemy populations (either through attraction or overall habitat stability) and I would anticipate that lady beetle, syrphids, anthocorids, and parasitoids would all benefit from margins that have been managed with this intent. Further research could explore the interaction of different margin treatments in pest and natural enemy abundance within celery fields.

In summary, I conclude that the margins in Michigan celery systems are not currently used to a large extent by most arthropod groups. Two arthropod groups seem to use them more than others: tarnished plant bugs and syrphid flies. Apart from these two groups, it does not seem likely that margins are a major source of insects that we find in the field. Furthermore, margin-centric patterns do not seem to be a reliable predictor of overall margin utilization (e.g. parasitoids) or abundance in the celery field, so care must be taken when making inferences based only on spatial abundance patterns.

APPENDICES

Appendix 1.1 Supplementary data

Table S1. The total number, frequency, and feeding functional group of arthropods captured on sticky traps in celery fields across southwest Michigan in 2013 and 2014. Frequency is percentage (%) of traps with at least one individual. "(Aq)" indicates aquatic taxa.

					2013		2014		
Order	**Suborder/ Superfamily**	**Superfamily/ Family**	**Sub-family/ group**	**Species**	**Total**	**Freq. (%)**	**Total**	**Freq. (%)**	**Feeding Functional Group**
Araneae					747	32.7	1088	43.2	Predator
Opiliones							2	0.2	Predator
Coleoptera		Anthicidae		*Notoxus* spp.	34	3.7	7	0.7	Detri/Herbivore
				Unidentified	164	12.4	3	0.4	Omnivore
		Buprestidae			2	0.2	4	0.5	Herbivore
		Cantharidae		*Chauliognathus* spp.			42	1.3	Predator
				Unidentified	16	2.0	73	7.2	
		Carabidae			148	11.6	60	6.1	Predator
		Chrysomelidae		*Acalymma vittatum*	7	0.9	7	0.8	Pest/Herbivore
				Cerotoma trifurcata	4	0.4	7	0.8	
				Diabrotica undecimpunctata			2	0.2	
				Oulema melanopus			7	0.7	
				Unidentified	452	17.5	316	20.5	
			Alticini	*Phyllotreta* spp.	39	2.8	73	5.5	
				Unidentified	720	26.1	1064	23.1	
			Cassidinae				15	0.8	
		Cleridae					2	0.2	
		Coccinellidae		*Coccinella septempunctata*	14	1.5	7	0.8	
				Coleomegilla maculata	347	26.6	363	23.9	
				Cycloneda munda	2	0.2	1	0.1	
				Harmonia axyridis	27	2.3	37	4.0	
				Hippodamia convergens	4	0.5	1	0.1	
				Hippodamia parenthesis	4	0.5	1	0.1	
				Hyperaspis spp.			1	0.1	
				Propylea quatuordecimpunctata	9	1.0			
				Psyllobora spp.			5	0.6	
				Scymnus spp.			253	15.8	
				Unidentified	12	1.5			
		Curculionidae	Dryophthorinae		137	12.4	111	10.3	Herbivore
			Scolytinae				2	0.2	Herbivore
		Elateridae					1	0.1	
		Histeridae			0	0.0	3	0.4	
		Lampyridae			9	1.0	8	0.9	
		Latridiidae			677	33.5	187	12.0	Fungivore
		Meloidae			4	0.2	1	0.1	
		Melyridae			0	0.0	6	0.5	
		Mordellidae			132	10.5	17	2.0	Herbivore/Predator
		Mycetophagidae					90	6.2	Fungivore
		Scarabaeidae			1	0.1	4	0.4	Herbivore

Table S1 (cont'd)

Order	Suborder/ Superfamily	Superfamily/ Family	Sub-family/ group	Species	2013 Total	2013 Freq. (%)	2014 Total	2014 Freq. (%)	Feeding Functional Group
		Silphidae					1	0.1	Detritivore
		Silvanidae					3	0.4	Fungivore
		Staphylinidae			452	30.3	350	26.9	
		Tenebrionidae			95	7.2			Detri/Herbivore
		Throscidae					4	0.5	Herbivore
		Unidentified			584	29.4	22	1.9	Various
Diptera		Asilidae			2	0.2	3	0.4	
		Chamaemyiidae			25	2.2	505	25.8	
		Dolichopodidae			0	0.0	225	19.0	
		Syrphidae			288	20.1	127	11.5	
		Tachinidae					124	9.2	Parasitoid
Ephemeroptera							1	0.1	Algivore (Aq)
Hemiptera	Auchenorryncha	Cercopidae			6	0.7	80	7.4	Herbivore
		Cicadellidae		*Empoasca fabae*	3582	75.5	6524	87.3	Pest/Herbivore
				Macrosteles quadrilineatus	2190	50.6	4174	51.6	
				Macrosteles spp. (other)			710	18.2	
				Agallia quadripunctata	9	0.3	166	11.3	
				Flexamia spp.			40	1.2	
				Norvellina spp.	1	0.1	1	0.1	
				Grape Leafhopper			29	1.6	
				Graphocephala coccinea			15	1.3	
				Colladonus clitellarius			5	0.6	
				Deltocephalus spp.			3	0.4	
				Draeculacephala zeae			8	0.8	
				Unidentified	1375	50.6	920	41.0	
		Issidae					1	0.1	Herbivore
		Membracidae			101	6.3	254	13.0	Herbivore
	Sternoryncha	Aphididae			28893	97.3	60938	90.8	Pest/Herbivore
		Aleyrodidae			983	23.3	627	40.6	Pest
		Psyllidae			238	14.6	676	30.0	Herbivore
	Heteroptera	Anthocoridae			313	18.3	416	25.4	Predator
		Berytidae					1	0.1	Herbivore
		Blissidae					1	0.1	Herbivore
		Cydnidae			3	0.4	39	1.5	Herbivore
		Lygaeidae		*Ischnodermus* spp.			2	0.2	
				Unidentified	2	0.1	1	0.1	
		Lygaeoidae			1	0.1	1	0.1	Herbivore
		Mesoveliidae					1	0.1	Herbivore
		Miridae		*Lygus lineolaris*	210	10.4	742	30.2	Pest/Herbivore

Table S1 (cont'd)

Order	Suborder/ Superfamily	Superfamily/ Family	Sub-family/ group	Species	2013 Total	2013 Freq. (%)	2014 Total	2014 Freq. (%)	Feeding Functional Group
				Lygus spp. (other)	202	7.4	265	13.3	
				Four-lined plant bug			12	0.8	
				Trigonotylus caelestialium	7	0.3	22	1.5	
				Plagiognathus spp.			11	1.2	
				Coccobaphes spp.			3	0.2	
				Halticus bractatus	5	0.1			
				Unidentified	185	13.7	177	12.2	
		Nabidae			11	0.9	5	0.5	Predator
		Pentatomidae			12	1.2	1	0.1	Herbivore
		Piesmatidae					27	2.6	Herbivore
		Reduviidae			2	0.3	1	0.1	Predator
		Saldidae					1	0.1	Predator
		Tingidae					6	0.7	Herbivore
		Unidentified			65	7.5	3	0.4	Herbivore
Hymenoptera		Formicidae			12	0.9	84	8.6	Predator
	Apoidea	Anthophila			1	0.1	11	1.2	Pollinator
		Colletidae	Hylaeinae				1	0.1	
			Unidentified				2	0.2	
		Sphecidae					20	2.0	
	Vespoidea	Tiphiidae					2	0.2	Parasitoid
		Pomilidae					1	0.1	Predator/parasitoid
		Vespidae					4	0.5	
		Unidentified			14	1.0	1	0.1	
	Aculeata	Unidentified			1	0.1	7	0.7	Predator
	Ichneumonoidea	Braconidae	Aphidiinae		16	1.7	136	9.5	Parasitoid
			Microgastrinae				5	0.6	
			Unidentified		184	16.4	520	35.1	
		Ichneumonidae			46	4.8	79	7.4	
		Unidentified			196	17.8	35	3.4	
	Chalcidoidea	Mymaridae			946	47.3	1591	67.6	
		Trichogrammatidae			185	15.3	448	31.7	
		Unidentified			1958	57.0	3581	75.6	
	Evanioidea	Evaniidae			1	0.1			
	Diaprioidea	Diapriidae					1	0.1	
	Ceraphronoidea	Ceraphronidae			33	2.3			
		Megaspilidae			1	0.1	29	2.8	
	Proctotrupoidea	Proctotrupidae					7	0.8	
	Chrysidoidea	Bethylidae			19	0.7	19	2.2	

Table S1 (cont'd)

					2013		2014		
Order	**Suborder/ Superfamily**	**Superfamily/ Family**	**Sub-family/ group**	**Species**	**Total**	**Freq. (%)**	**Total**	**Freq. (%)**	**Feeding Functional Group**
		Dryinidae					1	0.1	
	Cynipoidea	Unidentified			1244	39.2			
	Platigastroidea	Platygastridae					4	0.2	
		Scelionidae					1	0.1	
	Parasitica	Unidentified			593	29.0	6	0.7	
	Symphyta	Argidae		Purslane sawfly	13	0.5	25	1.3	Herbivore
				Unidentified	0		4	0.2	
		Siricidae			0		1	0.1	
		Tenthrendinidae			1	0.1	6	0.7	
	Unidentified				51	5.5	2	0.2	
Lepidoptera		Pieridae		*Pieris rapae*	10	1.1			Herbivore
				Phoebis sennae	1	0.1			
		Pyraloidea			1	0.1	6	0.7	
		Heterocera			15	3.1			
				Unidentified immature	0		5	0.5	
				Unidentified	11	1.2	73	7.5	
Neuroptera		Chrysopoidae			13	1.5	9	0.9	Predator
		Hemerobiidae			4	0.5	2	0.2	
Odonata	Anisoptera	Coenagrionidae					8	0.8	Predator
		Lestidae					2	0.2	
		Unidentified			6	0.7			
	Zygoptera	Libellulidae					3	0.4	
		Unidentified			37	3.8	6	0.7	
Orthoptera		Acrididae					13	1.4	Herbivore
		Tettigoniidae					3	0.4	
		Unidentified			16	1.3			
Plecoptera		Nemouridae			1	0.1	2	0.2	Detri/Algi/Herbivore (Aq)
		Unidentified			2	0.2			
Pscocoptera					164	11.8	76	6.3	Herbivore
Thysanoptera		Aeolothripidae		`	527	22.2	446	26.8	Predator
		Thripidae			23483	88.4	28736	97.1	Herbivore
Trichoptera		Unidentified			6	0.6	16	1.6	Various (Aq)

Table S2. Number analyzed (N), mean (+/- SEM) ELISA optical density value (OD), and the percentage of samples (%) testing positive for presence of albumin protein marker. Leaf samples were acquired before and after protein application to margins. Sticky trap sample discs were acquired from the recovered traps. Post-application tests of celery foliage and sticky traps were used to detect contamination resulting from wind drift, precipitation, or condensation.

Before Spraying

	Leaf type	N	OD Negative (mean +/- SEM)	N	OD Positive (mean +/- SEM)	%
Farm 1	*Chenopodium album*	4	0.095 ± 0.003	0	- -	0.0
	Portulaca oleracea	4	0.101 ± 0.001	0	- -	0.0
	Polygonum pensylvanicum	4	0.093 ± 0.001	0	- -	0.0
	Amaranthus spp.	4	0.103 ± 0.000	0	- -	0.0
	Ambrosia trifida	4	0.106 ± 0.004	0	- -	0.0
	Urtica dioica	4	0.109 ± 0.003	0	- -	0.0
	Grass (unknown)	4	0.103 ± 0.002	0	- -	0.0
	Celery (1st row)	4	0.102 ± 0.006	0	- -	0.0
Farm 2	*Arctium* spp.	4	0.105 ± 0.001	0	- -	0.0
	Typha spp.	4	0.096 ± 0.001	0	- -	0.0
	Urtica dioica	4	0.093 ± 0.001	0	- -	0.0
	Sassafras albidum	4	0.106 ± 0.004	0	- -	0.0
	Ascelpias syriaca	4	0.089 ± 0.000	0	- -	0.0
	Polygonum pensylvanicum	4	0.090 ± 0.001	0	- -	0.0
	Parthenocissus quinquefolia	4	0.091 ± 0.002	0	- -	0.0
	Celery (1st row)	4	0.095 ± 0.000	0	- -	0.0
Farm 3	*Convolvulus arvensis*	4	0.101 ± 0.002	0	- -	0.0
	Cyperus esculentus	4	0.102 ± 0.001	0	- -	0.0
	Silene Alba	4	0.105 ± 0.002	0	- -	0.0
	Abutilon theophrasti	4	0.102 ± 0.001	0	- -	0.0
	Amaranthus spp.	4	0.091 ± 0.001	0	- -	0.0
	Cirsium vulgare	4	0.104 ± 0.002	0	- -	0.0
	Ambrosia trifida	4	0.091 ± 0.001	0	- -	0.0
	Grass (unknown)	4	0.102 ± 0.006	0	- -	0.0
	Celery (1st row)	4	0.106 ± 0.003	0	- -	0.0

After Spraying

	Type	N	OD Negative (mean +/- SEM)	N	OD Positive (mean +/- SEM)	%
Farm 1	Celery (1st row)	7	0.093 ± 0.001	1	0.113 -	12.5
	Residue check	0	- -	4	0.750 ± 0.031	100.0
	Sticky trap check	4	0.089 ± 0.000	0	- -	0.0
Farm 2	Celery (1st row)	6	0.094 ± 0.001	2	0.099 ± 0.000	25.0
	Residue check	0	- -	4	0.637 ± 0.112	100.0
	Sticky trap check	4	0.086 ± 0.002	0	- -	0.0
Farm 3	Celery (1st row)	6	0.092 ± 0.001	2	0.105 ± 0.008	25.0
	Residue check	0	- -	8	0.435 ± 0.120	100.0
	Sticky trap check	4	0.089 ± 0.001	0	- -	0.0

Table S3. Number analyzed (N), mean (+/- SEM) ELISA optical density value (OD), and the percentage of individuals (%) testing positive for presence of albumin protein marker. All insects were collected from three different celery farms with sweep nets one week prior to protein marker application.

Taxon	N	OD (mean +/- SEM)	%
HEMIPTERA			
Anthocoridae	5	0.102 ± 0.002	0.0
Aphididae	7	0.091 ± 0.001	0.0
Macrosteles quadrilineatus	4	0.089 ± 0.001	0.0
Empoasca fabae	8	0.092 ± 0.001	0.0
Cicadellidae (other)	7	0.099 ± 0.002	0.0
Lygus lineolaris	16	0.099 ± 0.002	0.0
Lygus spp. (other)	2	0.102 ± 0.001	0.0
Miridae	1	0.084	0.0
Psyllidae	4	0.104 ± 0.003	0.0
Pentatomidae	2	0.110 ± 0.004	0.0
COCCINELLIDAE			
Propylea quatuordecimpunctata	2	0.091 ± 0.000	0.0
Coccinella septempunctata	1	0.110	0.0
Coleomegilla maculata	3	0.094 ± 0.003	0.0
Harmonia axyridis	1	0.120	0.0
Cycloneda munda	1	0.107	0.0
COLEOPTERA (Other)			
Cantharidae	4	0.092 ± 0.001	0.0
Carabidae	1	0.104	0.0
Chrysomelidae	11	0.094 ± 0.002	0.0
Curculionidae (weevil)	10	0.096 ± 0.002	0.0
ARANAE	8	0.100 ± 0.003	0.0
HYMENOPTERA			
Braconidae	12	0.100 ± 0.002	0.0
Ichneumonidae	2	0.104 ± 0.009	0.0
Chalcidoidea	8	0.100 ± 0.003	0.0
DIPTERA			
Chamaemyiidae	1	0.097	0.0
Syrphidae	14	0.100 ± 0.002	0.0
LEPIDOPTERA (moth)	5	0.097 ± 0.005	0.0

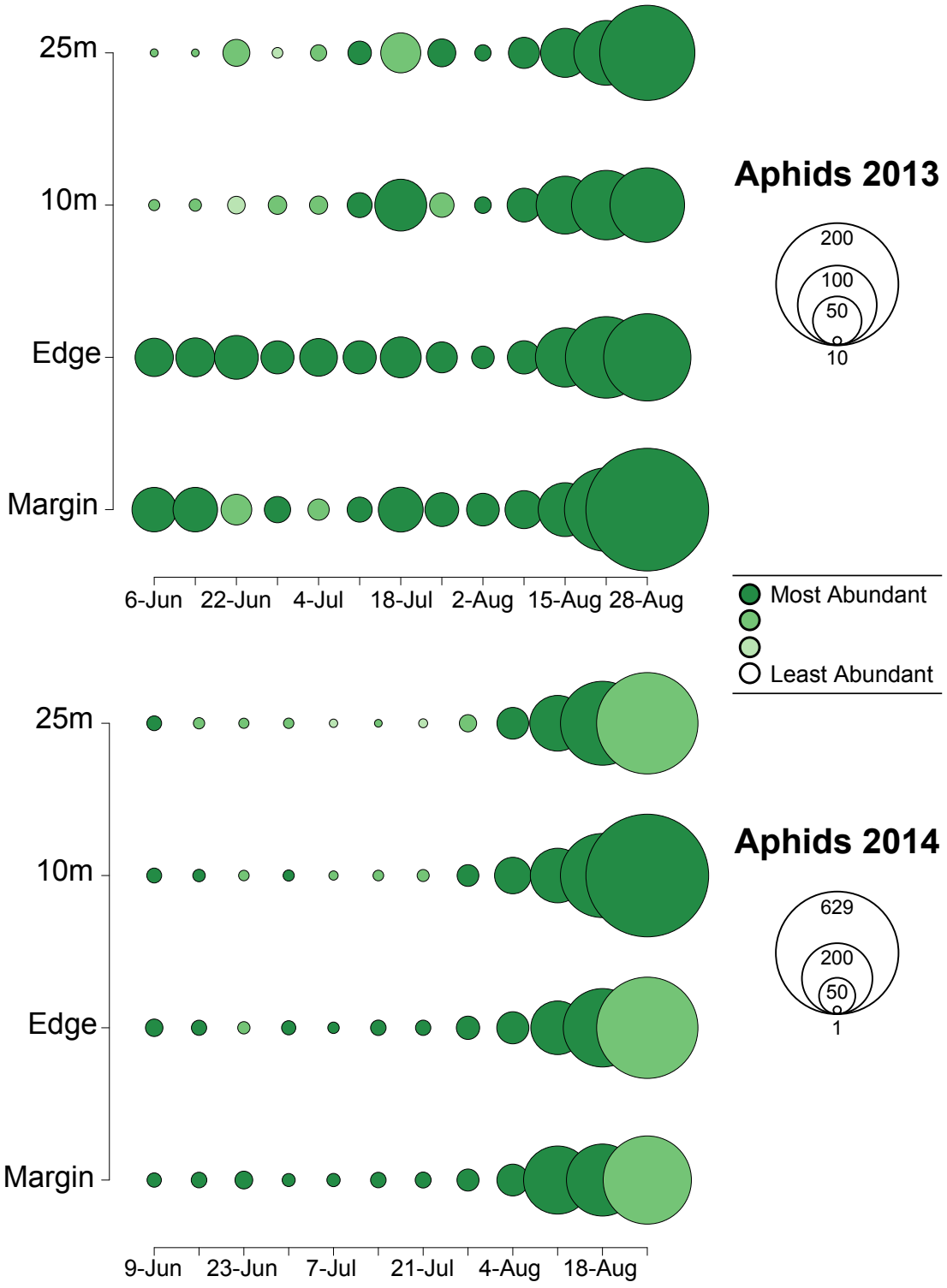

Figure S1. Mean distribution of alate aphids across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

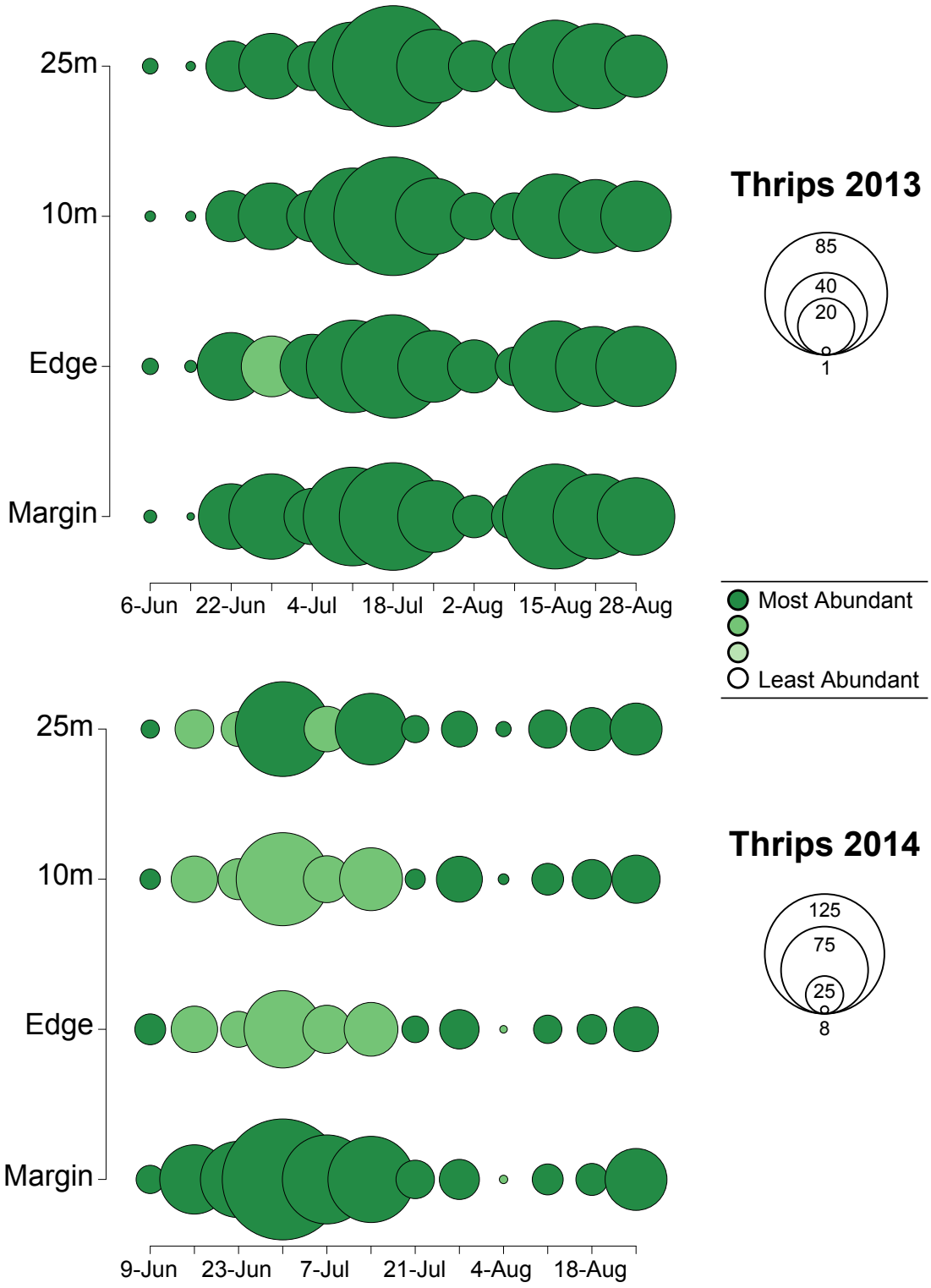

Figure S2. Mean distribution of thrips across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

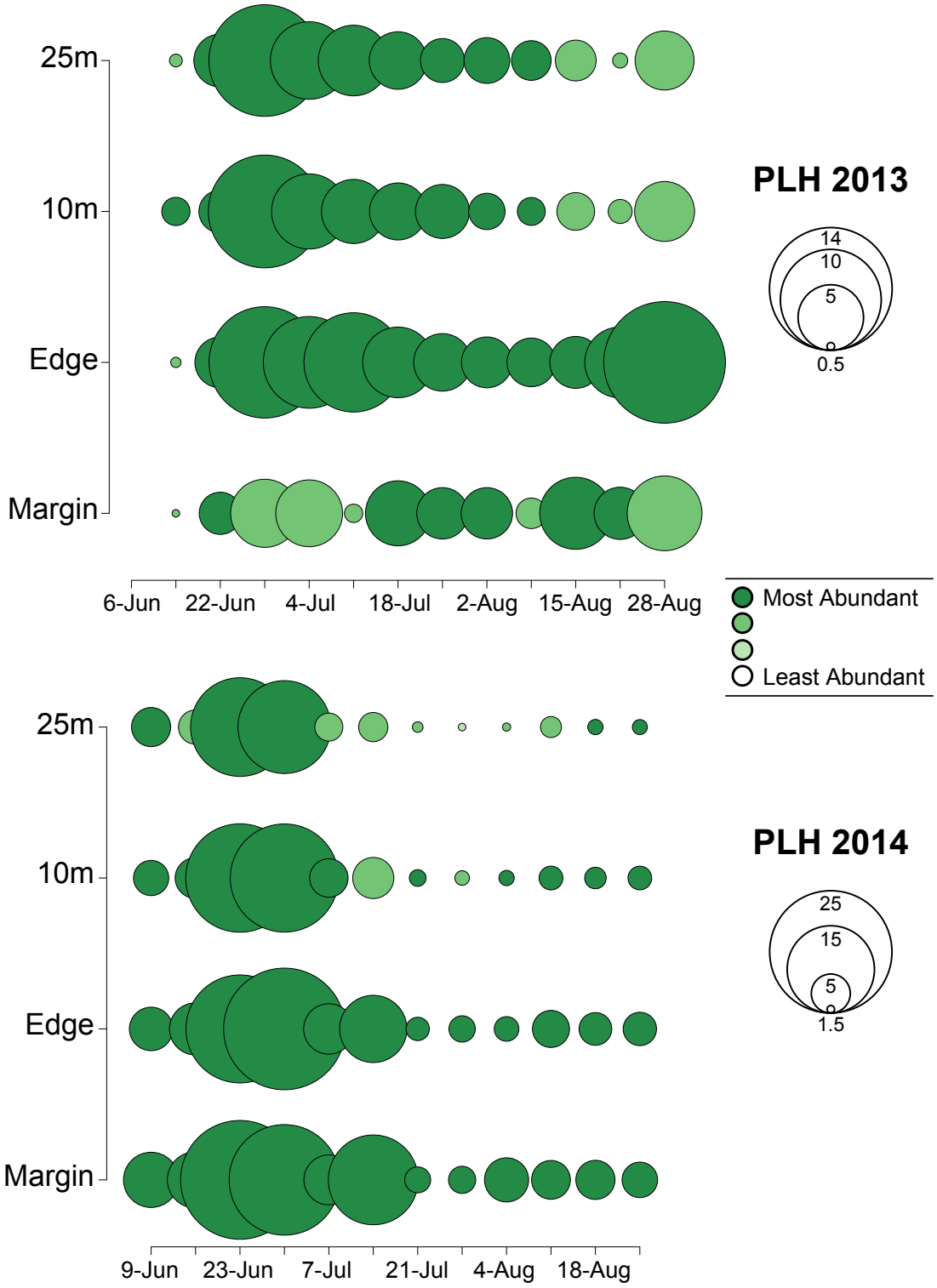

Figure S3. Mean distribution of potato leafhoppers across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

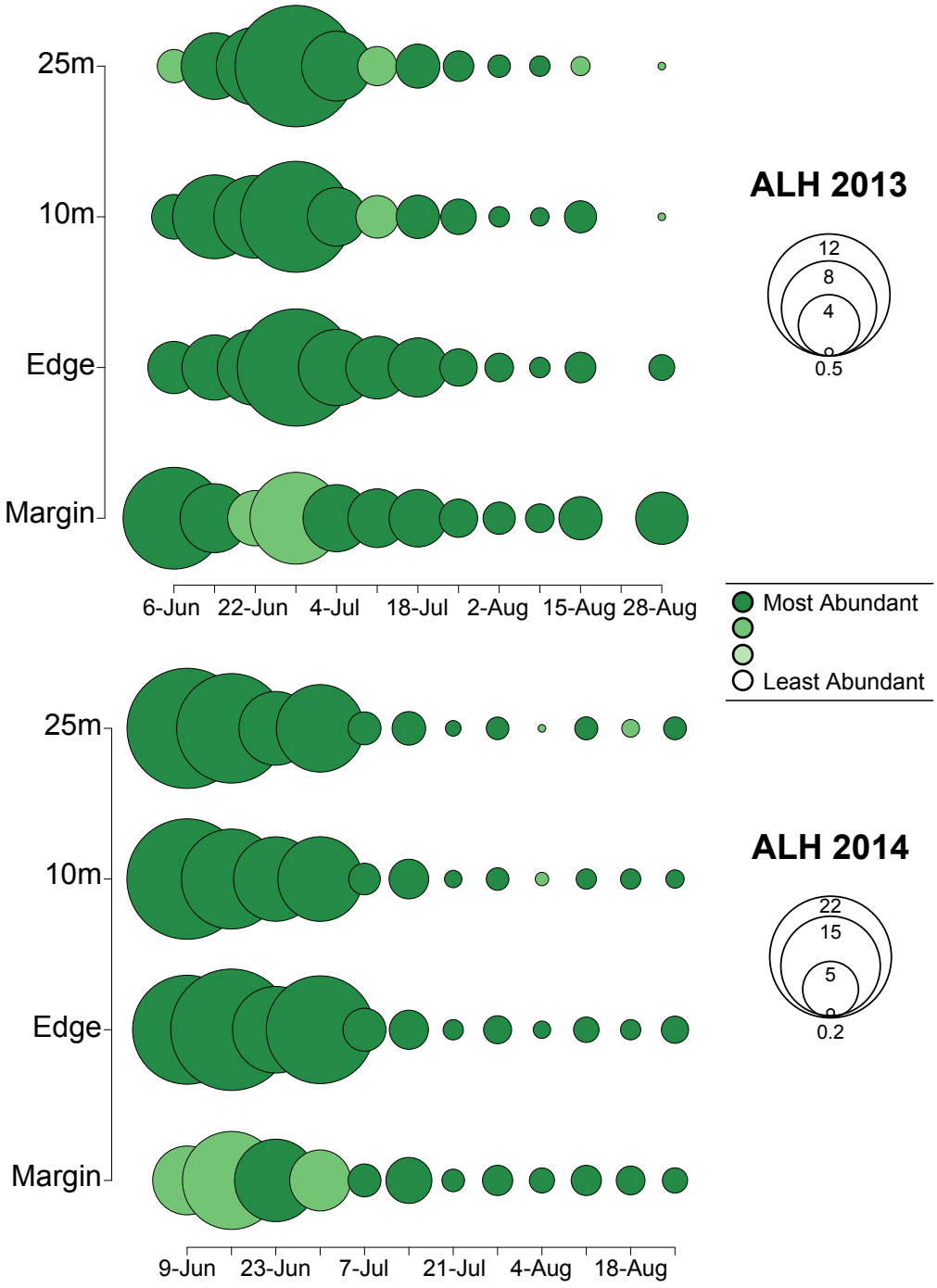

Figure S4. Mean distribution of aster leafhoppers across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

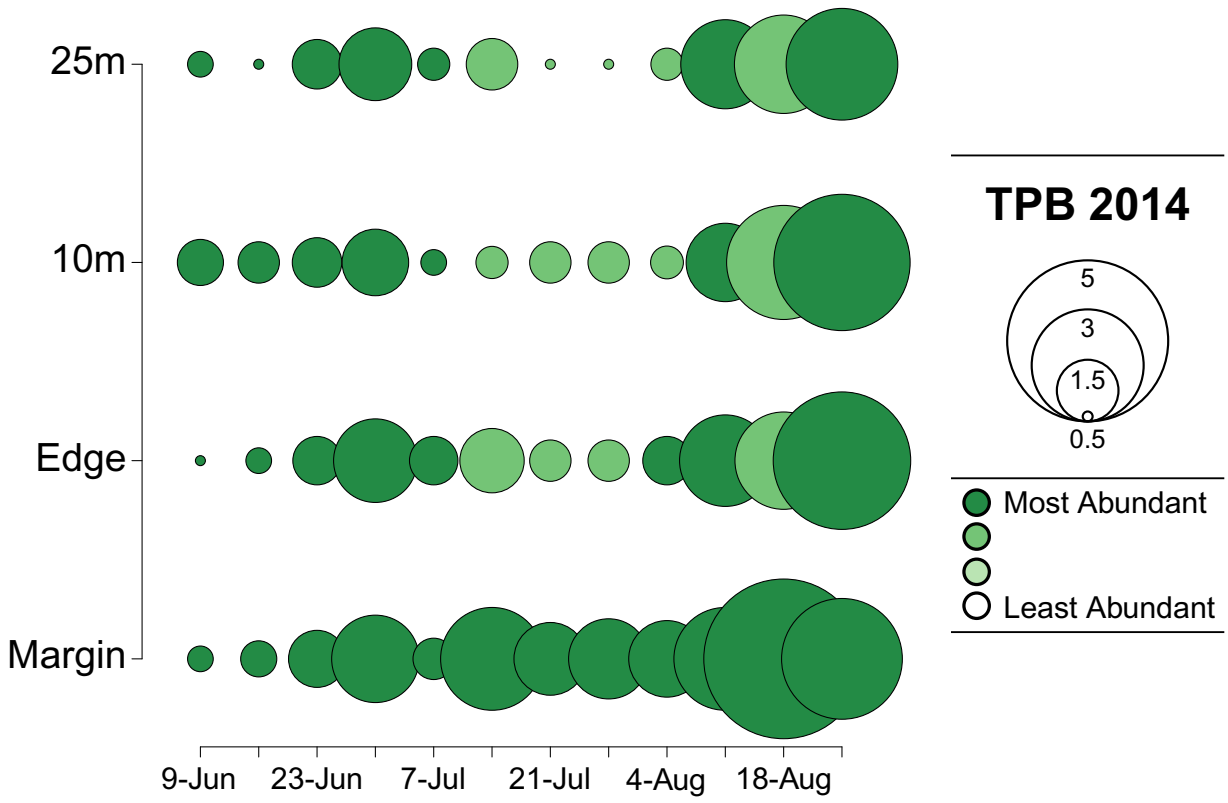

Figure S5. Mean distribution of tarnished plant bugs across four different sampling locations over all studied celery fields in southwest Michigan in 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

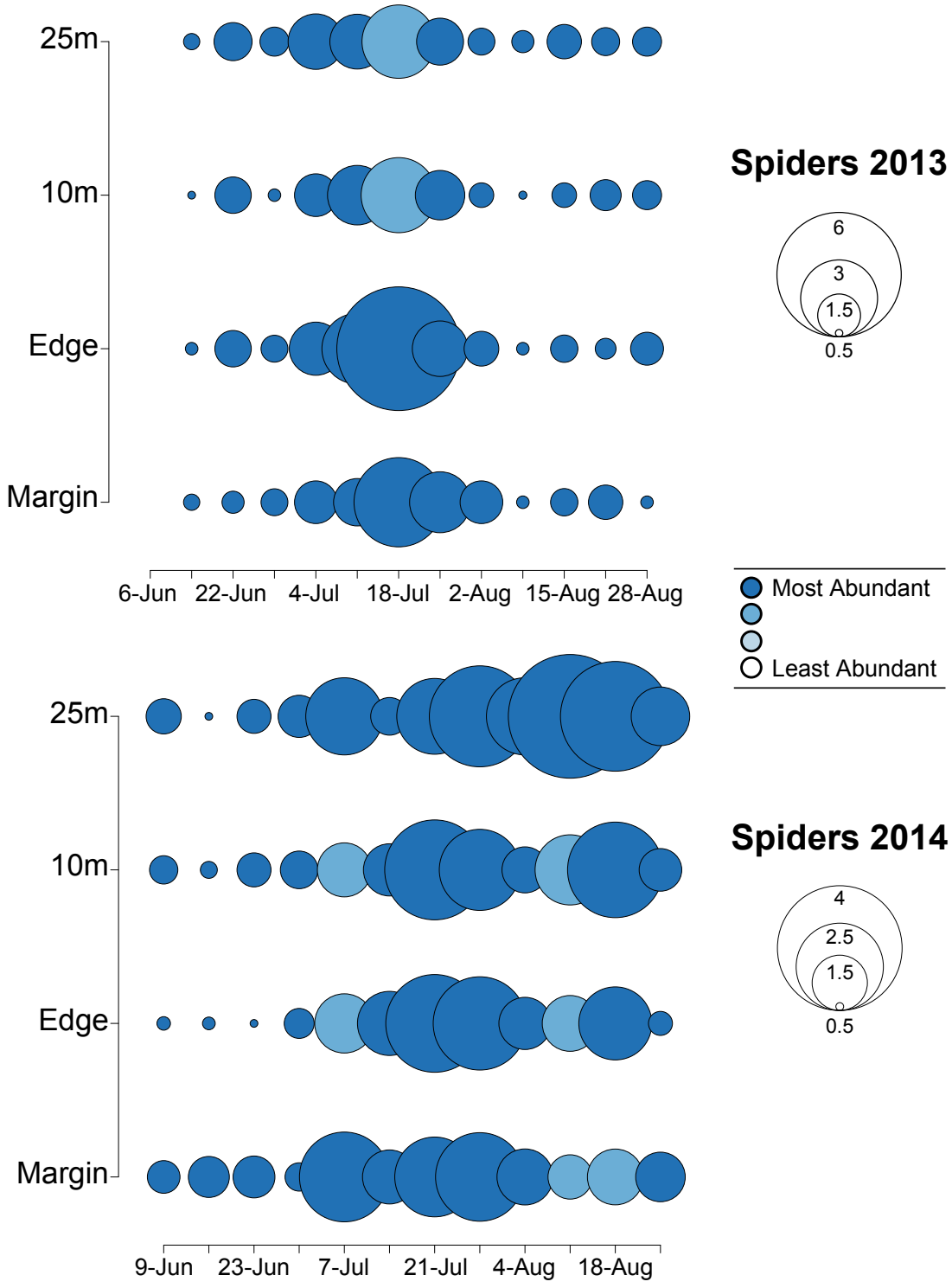

Figure S6. Mean distribution of spiders across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

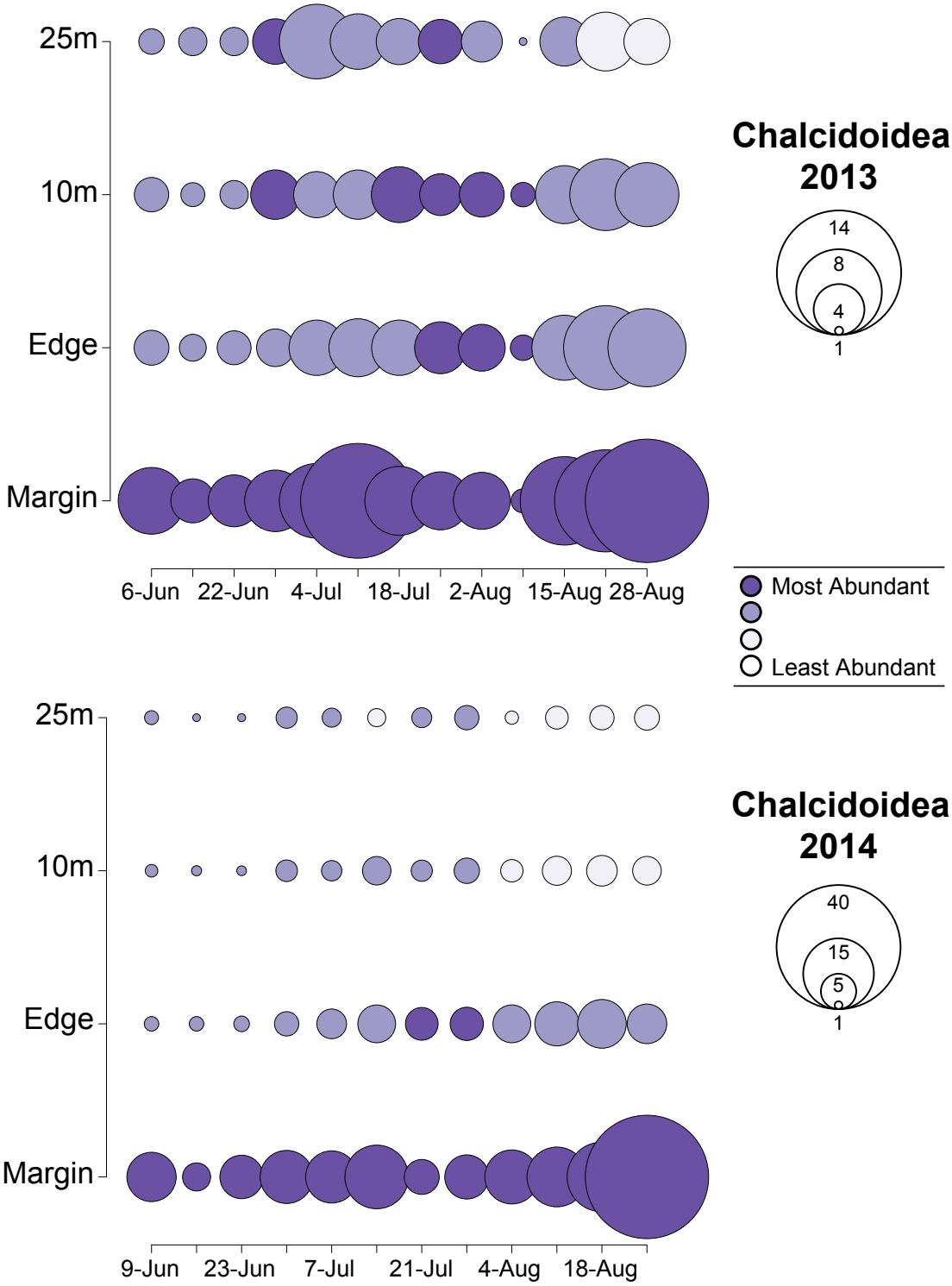

Figure S7. Mean distribution of chalcidoid wasps across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

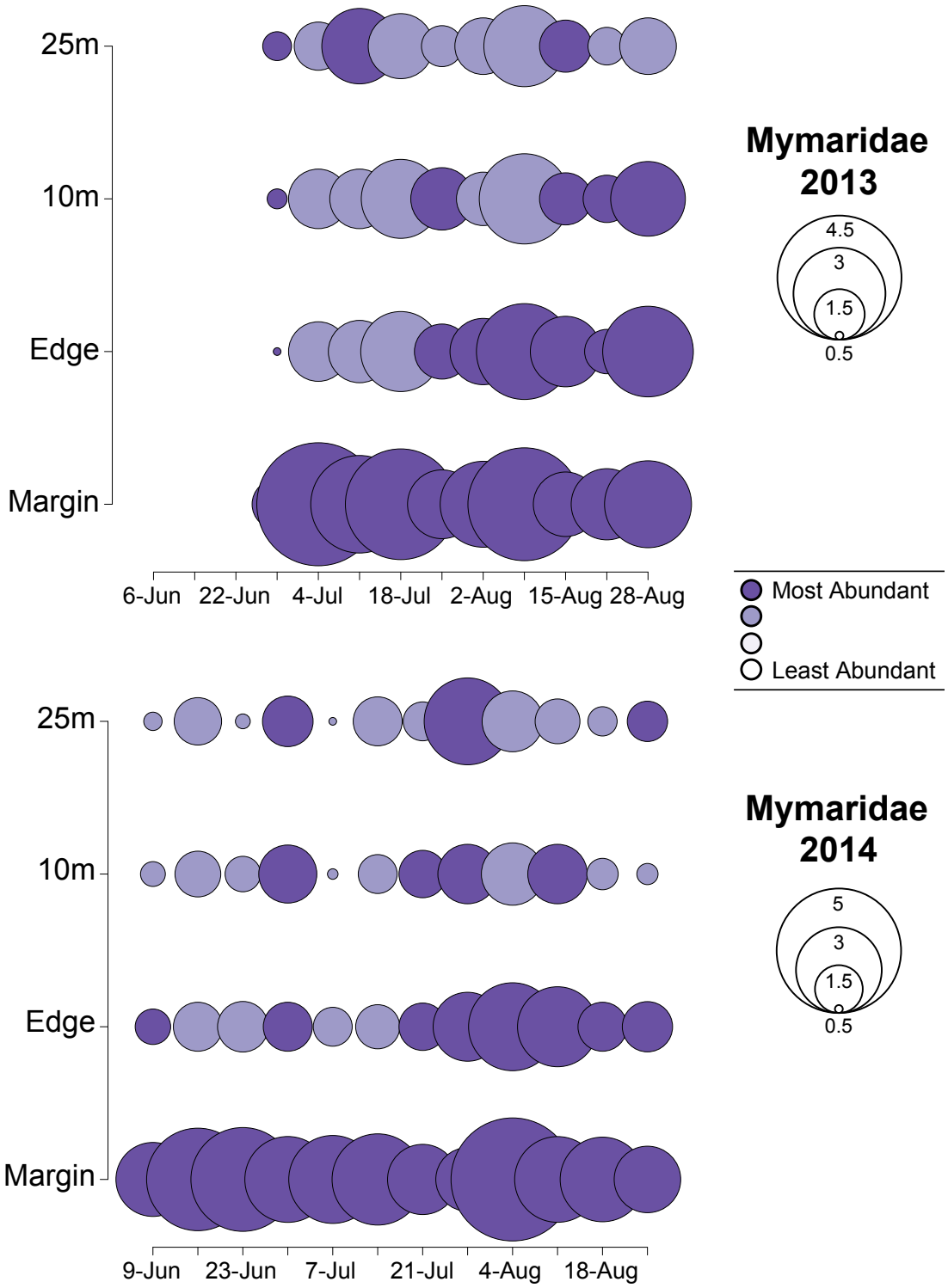

Figure S8. Mean distribution of mymarid wasps across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

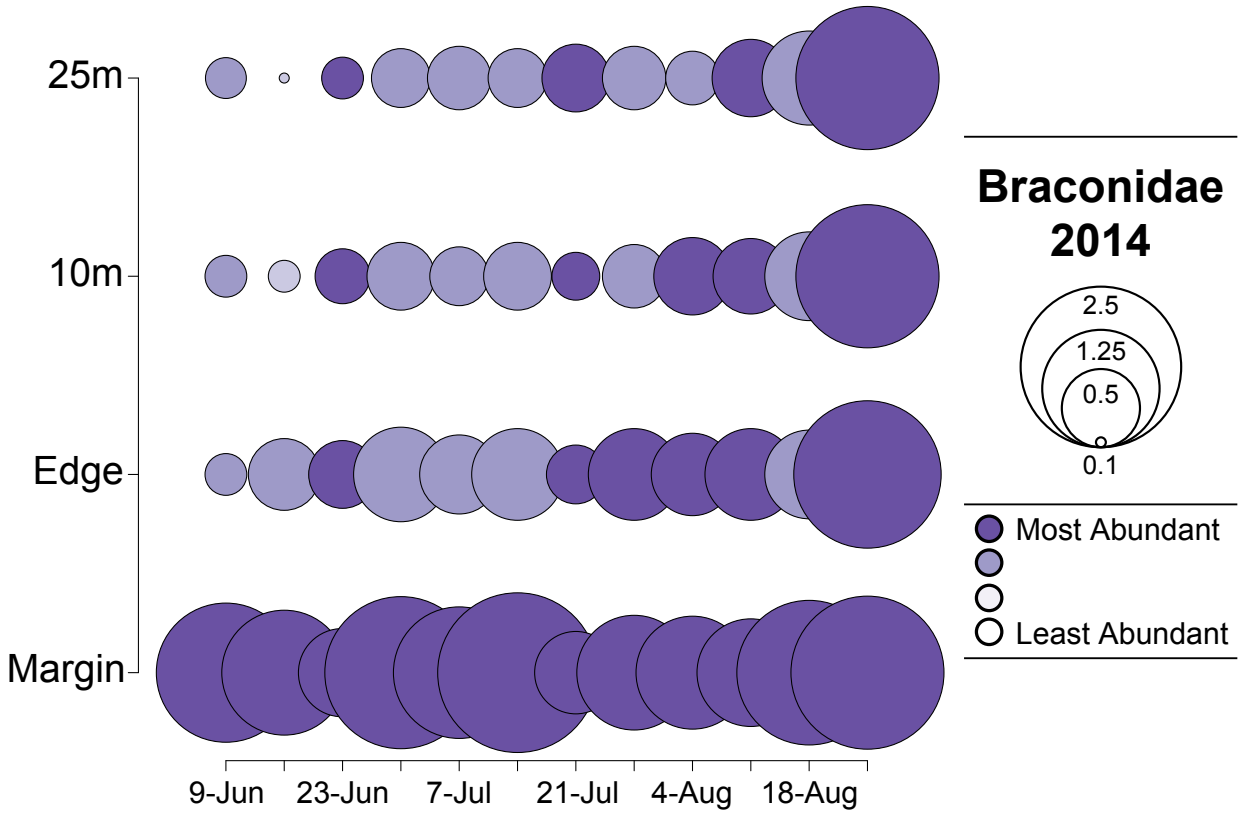

Figure S9. Mean distribution of braconid wasps across four different sampling locations over all studied celery fields in southwest Michigan for 2013 and 2014. Abundance is proportional to circle radius (mean aphids per sticky trap). Circles of the same color within weeks are not significantly different. Note: each year is at a different scale.

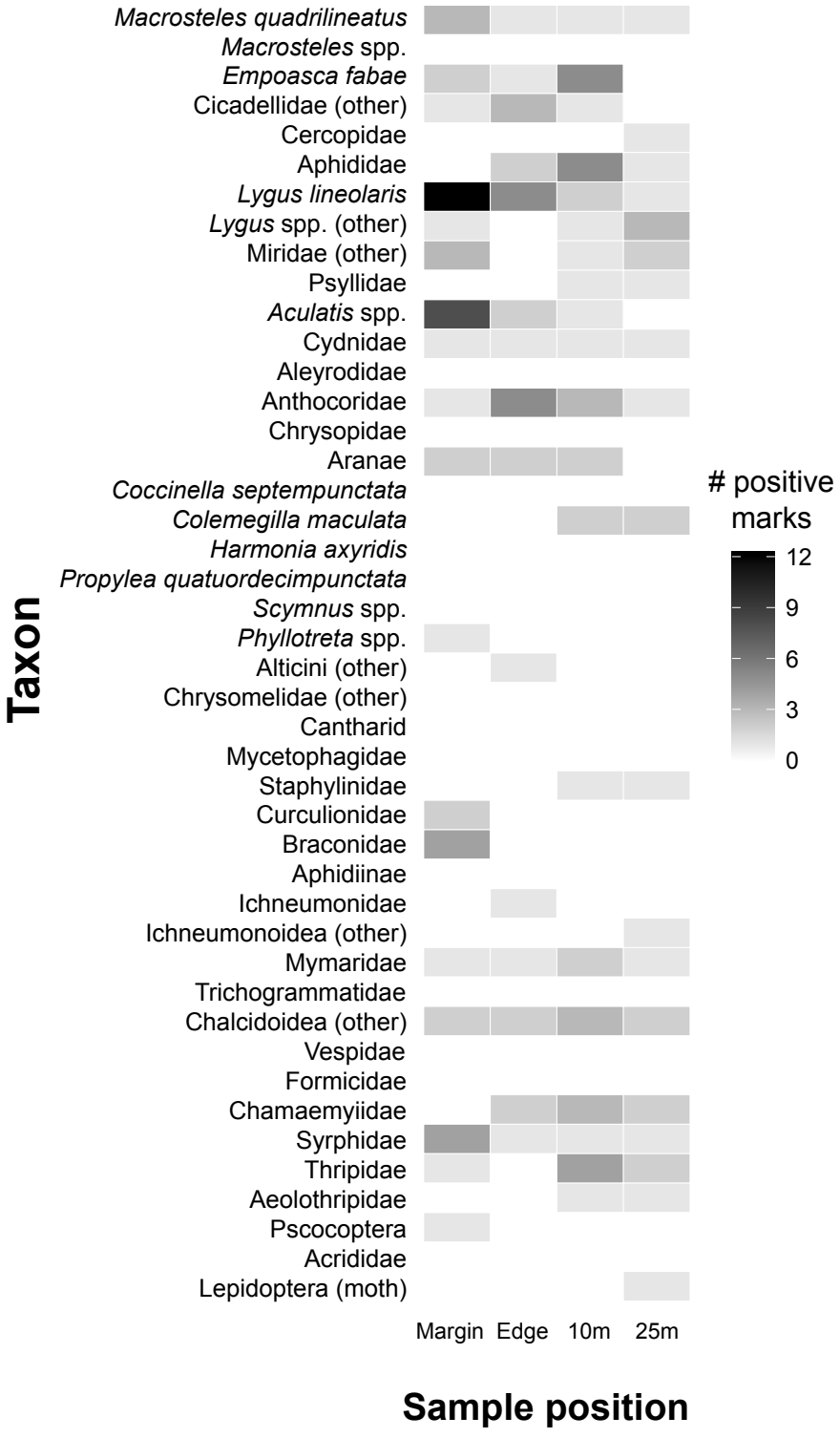

Figure S10. The number of individuals testing positive for the presence of a chicken egg protein marker applied to the margins of three celery fields in southwest Michigan.

Appendix 1.2

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: 2015-04

Author and Title of thesis:
Author: Jeremy Jubenville
Title: The spatial and temporal distribution of arthropods in Michigan celery agroecosystems

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

Specimens:
**If lowest taxonomic level is above family, lowest classification used for arthropod is indicated

Table S4. Voucher specimens deposited at the Albert J. Cook Arthropod Research Collection (Michigan State University).

Family	Genus-Species	Life Stage	Quantity	Preservation
Braconidae		Adult	4	Pinned
Chalcidoidea		Adult	7	Pinned
Chamaemyiidae		Adult	4	Pinned
Cicadellidae	*Macrosteles quadrilineatus*	Adult	4	Pinned
Coccinellidae	*Coleomegilla maculata*	Adult	2	Pinned
Miridae	*Lygus lineolaris*	Adult	3	Pinned

LITERATURE CITED

LITERATURE CITED

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems and the Environment 74: 19-31.

Atanassov, A. P. W. Shearer, G. Hamilton, and D. Polk. 2002. Development and implementation of a reduced risk peach arthropod management program in New Jersey. Journal of Economic Entomology 95: 803-812.

Bancroft, J. S. 2005. Dispersal and abundance of *Lygus hesperus* in field crops. Environmental Entomology 34: 1517-1523.

Beanland, L., L. V. Madden, C. W. Hoy, S. A. Miller, and L. R. Nault. 2005. Temporal Distribution of aster leafhopper sex ratios and spatial pattern of aster yellows phytoplasma disease in lettuce. Annals of the Entomological Society of America 98: 756-762.

Bianchi, F. J. J. A. and W. van der Werf. 2004. Model evaluation of the function of prey innon crop habitats for biological control of ladybeetles in agricultural landscapes. Ecological Modelling 171: 177-193.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. Roy. Soc. Lond. B 273: 1715–1727.

Blaauw, B. and R. Isaacs. 2012. Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density. Ecological Entomology 37: 386–394.

Blackman, R.L. and V.F. Eastop. 2007. Taxonomic Issues. pp. 1-29. *In* van Emden, H.F. and Harrington, R. (eds.) Aphids as Crop Pests. CABI, Wallingford, Oxon, UK.

Boersma, D. B., and W. H. Luckmann. 1970. Effects of tarnished plant bug feeding in soybean. J. Econ. Entomol. 63: 253--256.

Boivin, J.-P., R. Le Blanc, and J.A. Adams. 1991. Spatial dispersion and sequential sampling plan for the tarnished plant bug (Hemiptera: Miridae) on celery. Journal of Economic Entomology 84: 158-164.

Boina, D. R., W. L. Meyer, E. O. Onagbola, and L. L. Stelinksi. 2009. Quantifying dispersal of Diaphorina citri (Hemiptera: Psyllidae) by immunomarking and potential impact of unmanaged groves on commercial citrus management. Environmental Entomology 38: 1250-1258.

Brady, N. C. and R. R. Weil. 2007. Histosols. pp. 99-100. *In* The Nature and Properties of Soils (14th edition), Prentice Hall, Upper Saddle River, NJ.

Braun L., M. Erlandson, D. Baldwin, J. Soroka, P. Mason, R. Foottit, and D. Hegedus. 2001. Seasonal occurrence, species composition, and parasitism of Lygus spp. in alfalfa, canola, and mustard. The Canadian Entomologist 133: 565-577.

Buntin, G. D., L. P. Pedigo, and W. B. Showers. 1990. Temporal occurrence of the variegated cutworm (Lepidoptera: Noctuidae) adults in Iowa with evidence for migration. Environmental Entomology 19: 603-608.

Byrne, D. N. 1999. Migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. Agricultural and Forest Meteorology 97: 309-316.

Capinera, J. L. 2001. Handbook of Vegetable Pests. Academic Press (Elsevier), San Diego, CA.

Christensen, N. M., K. B. Axelsen, M. Nicolaisen, and A. Schultz. 2005. Phytoplasmas and their interactions with hosts. Trends in Plant Science 10: 526-535.

CIE (Commonwealth Institute of Entomology)**. 2001.** Distribution Maps of Pests, No. 256. CAB International, Wallingford, Oxon, UK.

Clancy, D. W. and H. D. Pierce. 1966. Natural enemies of some lygus bugs. Journal of Economic Entomology 59: 853-858.

Collinge, S.K. 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement Patterns. Ecology 81: 2211-2226.

Conradt, L. and T. J. Roper. 2006. Nonrandom movements behaviour at habitat boundaries in two butterfly species: implications for dispersal. Ecology 87: 125–132.

Cook, W. C., K. T. Lane, B. L. Foster, and R. D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters 5:619–623.

Cowgill, S. E., S. D. Wratten, and N. W. Sotherton. 1993. The effect of weeds on the numbers of hoverfly (Diptera: Syrphidae) adults and the distribution and composition of their eggs in winter wheat. Annals of Applied Biology 123: 499-515.

Cronin, J. T. 2009. Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. Ecology 90: 196-207.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14: 342–355.

Delattre, T., J-B. Pichancourt, F. Burel, P. Kindlmann. 2010. Grassy field margins as potential corridors for butterflies in agricultural landscapes: A simulation study. Ecological Modelling 221: 370-377.

Dillard, H. R. 1992. *Colletotrichum coccodes*: the pathogen and its hosts. pp 225-236. In *Colletotrichum*: Biology, Pathology and Control, J. A. Bailey and M. J. Jeger, eds. CAB International, Wallingford, Oxon, UK.

Dixon, A. F. G. 1977. Aphid Ecology - Life-cycles, polymorphism, and population regulation. Annual Review of Ecology and Systematics 8: 329-353.

Dixon, A. F. G. 1985. Aphid ecology. Blackie & Son Ltd., Glasgow, Scotland, UK**.**

Duffield, S. T. and N. J. Aebischer. 1994. The effect of spatial scale of treatment with dimethoate on invertebrate population recovery in winter wheat. Journal of Applied Ecology 31: 263-281.

Emmen, D. A., S. J. Fleischer, and A. Hower. 2004. Temporal and spatial dynamics of *Empoasca fabae* (Harris) (Homoptera: Cicadellidae) in Alfafa. Environmental Entomology 33: 890-899.

Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8: 50–59.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics 34: 487-515.

Fleischer, S. J. and M. J. Gaylor. 1987. Seasonal abundance of *Lygus lineolaris* (Heteroptera: Miridae) and selected predators in early season uncultivated hosts: implications for managing movement into cotton. Environmental Entomology 16: 379-389.

Foshee, W. G., R. T. Boozer, E.K. Blythe, D.L. Horton, J. Burkett. 2008. Management of plum curculio and catfacing insects on peaches in central Alabama: standard crop stage-based vs. integrated pest management-based approaches. International Journal of Fruit Science 8: 188-199.

Freeman Long, R., A. Corbett, C. Lamb, C. Reberg-Horton, J. Chandler, and M. Stimmann. 1998. Beneficial insects move from flowering plants to nearby crops. California Agriculture 52: 23–26.

Frost,K.E., D. K. Willis, and R. L. Groves. 2011. Detection and Variability of Aster Yellows Phytoplasma Titer in Its Insect Vector, *Macrosteles quadrilineatus* (Hemiptera:Cicadellidae). Journal of Economic Entomology 104: 1800-1815.

Grafius, E. and E. A. Morrow. 1982. Damage by the tarnished plant bug and alfalfa plant bug (Heteroptera: Miridae) to asparagus. Journal of Economic Entomology 75: 882-884.

Graham, H. M., C. G. Jackson, and J. W. Debolt. 1986. *Lygus* spp. (Hemiptera: Miridae) and their parasites in agricultural areas of southern Arizona. Environmental Entomology 15: 132-142.

Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. The American Naturalist 153: 215-227.

Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. Ecology 84: 609-615.

Hagler, J. R. and V. P. Jones. 2010. A protein-based approach to mark arthropods for mark-capture type research. Entomologia Experimentalis et Applicata 135: 177-192.

Hagler, J. R. 2011. An immunological approach to quantify consumption of protein-tagged *Lygus hesperus* by the entire cotton predator assemblage. Biological Control 58: 337-345.

Halbert, S.E. and D.J. Voegtlin. 1992. Morphological differentiation between *Aphis spiraecola* and *Aphis pomi* (Homoptera: Aphididae). The Great Lakes Entomologist 25: 1-8.

Hanski, I. 1998. Metapopulation dynamics. Nature 396: 41-48.

Hausbeck, M. 2011. Pest management in the future: a strategic plan for the Michigan celery industry. USDA Regional Pest Management Centers, Center Products/PMSPs. Online.

Hickman, J. M. and S. D. Wratten. 1996. Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by overfly larvae in cereal fields. Journal of Economic Entomology 89: 832-840.

Hilbe, J. M. 2014. Modeling Count Data. Cambridge University Press, New York, NY.

Hodek, I., G. Iperti, and M. Hodkova. 1993. Long distance flights in Coccinellidae (Coleoptera). European Journal of Entomology 90: 404-414.

Hogmire, H. W., H. W. Brown, J. J. Schmidt, and T. M. Winfield. 1992. Population development and insecticide susceptibility of apple aphid and spirea aphid (Homoptera: Aphididae) on apple. Journal of Entomological Science 27: 113-119.

Holt, R. D., 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs, R.E., D. Schluter (eds.), Species diversity in ecological communities. University of Chicago Press, Chicago, IL, USA, pp. 77–88.

Holt, R. D. 2002. Food webs in space: On the interplay of dynamic instability and spatial processes. Ecological Research 17: 261-273.

Holt, R. D., J. H. Lawton, G. A. Polis, and N. D. Martinez. 1999. Trophic rank and the species–area relationship. Ecology 80: 1495–1504.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2009. Grass strip corridors in agricultural landscapes enhance nest-site colonization by solitary wasps. Ecological Applications 19: 123-132.

Horton, D. R., V. P. Jones, and T.R. Unruh. 2009. Use of a new immunomarking method to assess movement by generalist predators between a cover crop and tree canopy in a pear orchard. American Entomologist 55: 49-56.

Hoy, C. W., S. E. Heady, and T. A. Koch. 1992. Species composition, phenology, and possible origins of leafhoppers (Cicadellidae) in Ohio vegetable crops. Journal of Economic Entomology 85: 2336-2343.

Janzen, D. H. 1983. No park is an island: increase interference from outside as park size decreases. Oikos 41: 402–410.

Jones, V. P., J. R. Hagler, J. F. Brunner, C. C. Baker, T. D. Wilburn. 2006. An inexpensive immunomarking technique for studying movement patterns of naturally occurring insect populations. Environmental Entomology 35: 827-836.

Jones, V. P., T. D. Melton, and C. C. Baker. 2011. Optimizing immunomarking systems and development of a new marking system based on wheat. Journal of Insect Science 11: 1-16.

Jonsen, I. D. and L. Fahrig. 1997. Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology 12: 185–197.

Kelton, L. A. 1975. The Lygus bugs (Genus *Lygus* Hahn) of North America (Heteroptera: Miridae). Memoirs Entomological Society of Canada 95: 1-101.

Kennedy, J. S. 1985. Migration, behavioural and ecological. pp 5-26. *In* Rankin, M.A. (ed.) Migration: Mechanisms and Adaptive Significance. Contributions in Marine Science Supplement Vol. 27.

Khattat, A. R. and R. K. Stewart. 1975. Damage by tarnished plant bug to flowers and setting pods of green beans. Journal of Economic Entomology 68: 633-635.

Krauss, J., I. Steffan-Dewenter and T. Tscharntke. 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? Journal of Biogeography, 30, 889–900.

Krishnamurthy, K. S. 2008. Celery, pp 401-412. In Parthasarathy, V.A., Chempakam, B., and Zachariah, T. J., (eds.) Chemistry of Spices. CABI Publishing, Wallingford, Oxon, UK.

Kruess, A. and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science 264: 1581–1584.

Lacy, M. L., R.D. Berger, R.L. Gilberson, and E.L. Litle. 1996. Current challenges in controlling diseases of celery. Plant Disease 80:1084-1091.

Landis, D. & P. Marino. 1999. Landscape structure and extrafield processes: impact on management of pests and beneficials. pp 79–104. In J. R. Ruberson (ed.) Handbook of pest management, Marcel Dekker Inc, New York, NY.

Landis, D.A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology 45: 175–201.

Lavandero, A., S. Wratten, J. Hagler, and M. Jervis. 2004. The need for effective marking and tracking techniques for monitoring the movements of insect predators and parasitoids. International Journal of Pest Management 50: 147-151.

Lee, J. C., F. D. Menalled, and D. A. Landis. 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. Journal of Applied Ecology 38: 472-483.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7: 601–613.

Leigh, T. F. and D. Gonzalez. 1976. Field cage evaluation of predators for control of *Lygus hesperus* Knight on cotton. Environmental Entomology 5: 948-952.

Levine, R. L. 2013. Celery, pp. 245-248. *In* Cumo, Christopher (ed.) Encyclopedia of Cultivated Plants. ABC-CLIO, Santa Barbara, CA.

Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237–240.

Lindbo, D. L. and D. A. Kozlowski. 2005. Histosols, pp. 830-834. *In* Lal, Rattan (ed.) Encyclopedia of Soil Science (2nd edition), CRC Press, Boca Raton, FL.

Lowery, T., R. Footit, M. Smirle, and E. Peryea. 2002. Identification, biology, and insecticide resistance of green apple aphid and spirea aphid. pp 148-156. *In* Entomology Research Review. Washington Tree Fruit Research Commission. Yakima, WA.

Lucas, R. E. 1982. Organic soils (Histosols) formation, distribution, physical, and chemical properties and management for crop production. *In* Farm Science Research Report 435, Michigan State University Agricultural Experiment Station, East Lansing, MI

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Marino, P. C. and D. A. Landis. 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. Ecological Applications 6: 276–284.

Meade, A. B., and A. G. Peterson. 1964. Origin of populations of the six-spotted leafhopper, *Macrosteles fascifrons*, in Anoka County, Minnesota. J. Economic Entomology 57: 885-8.

Morrison III, W. R. and Z. Szendrei. 2013. Patterns of Spatial and Temporal Distribution of the Asparagus Miner (Diptera: Agromyzidae): Implications for Management. Journal of Economic Entomology 106: 1218-1225.

Nicholls, C. I., M. Parrella, and M. A. Altieri. 2001. The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. Landscape Ecology 16: 133–146.

Norton, A. P., S. C. Welter, J. L. Flexner, C. G. Jackson, J. W. Debolt, and C. Pickel. 1992. Parasitism of *Lygus hesperus* (Miridae) by *Anaphes iole* (Mymaridae) and *Leiophron uniformis* (Braconidae) in California Strawberry. Biological Control 2: 131-137

Peck, G. W., H. J. Ferguson, V. P. Jones, S. D. O'Neal, and D. B. Walsh. 2014. Use of a highly sensitive immunomarking system to characterize face fly (Diptera: Muscidae) dispersal from cow pats. Environmental Entomology 43: 116-122.

Peres, N. A., L. W. Timmer, J. E. Adaskaveg, and J. C. Correll. 2005. Lifestyles of *Colletotrichum acutatum*. Plant Dis. 89:784-796.

Pickett, C. H., S. L. Swezey, D. J. Nieto, J. A. Bryer, M. Erlandson, H. Goulet, and M. D. Schwartz. 2009. Colonization and establishment of *Peristenus relictus* (Hymenoptera: Braconidae) for control of *Lygus* spp. (Hemiptera: Miridae) in strawberries on the California Central Coast. Biological Control 49: 27-37.

Poston, F. L. and L. P. Pedigo. 1975. Migration of plant bugs and the potato leafhopper in a soybean-alfalfa complex. Environmental Entomology 4: 8-10.

Pulliam, H. R., 1988. Sources, sinks, and population regulation. American Naturalist 132: 652–661.

Rand, T. A. and S. M. Louda. 2006 Spillover of Agriculturally Subsidized Predators as a Potential Threat to Native Insect Herbivores in Fragmented Landscapes. Conservation Biology 20: 1720–1729.

Rand, T., J. M. Tylianakis, and T. Tscharntke. 2006. Spillover edge effects: the dispersal of agriculturally-subsidized insect natural enemies into adjacent natural habitats. Ecology Letters 9: 603–614.

Ridgeway, R. L. and G. G. Gyrisco. 1960. Effect of temperature on the rate of development of *Lygus lineolaris* (Hemiptera: Miridae). Annals of the Entomological Society of America 53: 691-694.

Rodríguez-Salamanca, L. M., T. B. Enzenbacher, J. M. Byrne, C. Feng, J. C. Correll, and M. K. Hausbeck. 2012. First report of *Colletotrichum acutatum* causing leaf curling and petiole anthracnose on celery (*Apium graveolens*) in Michigan. Plant Disease 96:1383.

Rosch, V., T. Tscharntke, C. Scherber, and P. Batary. 2013. Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. Journal of Applied Ecology 50: 387-394.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

Scales, A. L. 1973. Parasites of the Tarnished Plant Bug in the Mississippi Delta. Environmental Entomology 2: 304-306.

Schaeffers, G. A. 1980. Yield effects of tarnished plant bug feeding on June-bearing strawberry varieties in New York State. Environmental Entomology 73: 721–725.

Schellhorn, N. A., F. J. J. A. Bianchi, and C.L. Hsu. 2014. Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. Annual Review of Entomology 59: 559-81.

Schowalter, T. D. 2012. Insect responses to major landscape-level disturbance. Annual Review of Entomology 57: 1–20.

Seymour, L. M., T. M. Mowry, W. H. Day, and J. D. Barbour. 2005. Parasitism of *Lygus* spp. nymphs by the parasitoid wasp, *Peristenus howardi*, in the alfalfa seed-growing region of the Pacific Northwest. Journal of Insect Science 5: 1-8.

Shmida, A. and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography 12: 1-20.

Smirle, M. J. C. L. Zurowski, D. T. Lowery, and R. G. Footit. 2010. Relationship of Insecticide Tolerance to Esterase Enzyme Activity in *Aphis pomi* and *Aphis spiraecola* (Hemiptera: Aphididae). Journal of Economic Entomology 103: 374-378.

Snodgras, G. L., W. P. Scott, and J. W. Smith. 1984. Host Plants and Seasonal Distribution of the Tarnished Plant Bug (Hemiptera: Miridae) in the Delta of Arkansas, Louisiana, and Mississippi. Environmental Entomology 13: 110-116.

Snodgrass, G. L., W. P. Scott, C. A. Abel, J. T. Robbins, J. Gore, and D. D. Hardee. 2005. Tarnished Plant Bug (Heteroptera: Miridae) Populations near fields after early season herbicide treatment. Environmental Entomology 34: 705-711.

Steffan-Dewenter I, U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale dependent effects of landscape structure on three pollinator guilds. Ecology 83: 1421–32.

Stewart, R. K. and H. Khoury. 1976. The biology of *Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae) in Quebec. Annals of the Entomological Society of Quebec 21: 52-63.

Suter, R. B. 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. Journal of Arachnology 27: 281-293.

Swezey, S. L., D. J. Nieto, and J. A. Bryer. 2007. Control of western tarnished plant bug *Lygus hesperus* Knight (Hemiptera: Miridae) in California organic strawberries using alfalfa trap crops and tractor-mounted vacuums. Environmental Entomology 36: 1457-1465.

Swezey, S. L., D. J. Nieto, J. R. Hagler, C. H. Pickett, J. A. Bryer , and S. A. Machtley. 2013. Dispersion, Distribution, and Movement of *Lygus* spp. (Hemiptera: Miridae) in Trap-Cropped Organic Strawberries. Environmental Entomology 42: 770-778.

Taylor, L. R. 1974. Insect migration, flight periodicity, and the boundary layer. Journal of Animal Ecology 43: 225-238.

Thies, C., I. Steffan-Dewenter, T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101: 18–25.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75: 2–16.

Tscharntke T, I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecological Applications 12:354–63.

Tscharntke, T. and R. Brandl. 2004. Plant-insect interactions in fragmented landscapes. Annual Review of Entomology 49: 405-430.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005a. Landscape perspectives on agricultural intensification and biodiversity –ecosystem service management. Ecology Letters 8: 857–874.

Tscharntke, T., T. A. Rand, and F. J. J. Bianchi. 2005b. The landscape context of trophic interactions: insect spillover across the crop–noncrop interface. Ann. Zool. Fennici 42: 421–432.

Tscharntke T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control 43: 294-309.

Tylianakis, J. M., A. M. Klein, and T. Tscharntke. 2005. Spatiotemporal variation in the effects of a tropical habitat gradient on Hymenoptera diversity. Ecology 86: 3296–3302.

Tylianakis, J. M., A. M. Klein, T. Lozada, and T. Tscharntke, 2006. Spatial scale of observation affects α, β, and γ, diversity of cavity-nesting bees and wasps across a tropical land-use gradient. Journal of Biogeography 33: 1295–1304.

Van Dyck, H. and M. Baguette. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? Basic and Applied Ecology 6: 535–545.

van Helden, M. 2010. Spatial and Temporal Dynamics of Arthropods in Arable Fields. pp. 55-64. In Oerke, E-C., Gerhards, R., Gunter, M., and Sikora, R.A. (eds.) Precision crop protection - the challenge and use of heterogeneity. Springer, Dordrecht, Heidelberg, London, New York.

van Nouhuys, S. and I. Hanski. 2002. Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. Journal of Animal Ecology 71: 639–650.

Wagge, J. K. 1978. Arrestment responses of the parasitoid, *Nemeritis canescens*, to a contact chemical produced by its host, *Plodia interpunctella*. Physiological Entomology 3: 135-146.

Wagge, J. K. 1979. Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. Journal of Animal Ecology 48: 353-371.

Wackers, F. L. 2001. A comparison of nectar and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. Journal of Insect Physiology 47: 1077–1084.

Wackers, F. L. 2004. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. Biological Control 29: 307–314.

Wallis, E. L. 1962. Host plant preference of the six-spotted leafhopper. Journal of Economic Entomology 55: 998-999.

Webber, D. C. and J. G. Lundgren. 2009. Assessing the trophic ecology of the Coccinellidae: Their roles as predators and as prey. Biological Control 51:199-214.

Westdal P. H., C. F. Barrett, H. P. Richardson. 1961. The six-spotted leafhopper, *Macrosteles fascifrons* (STÅL.) and Aster Yellows in Manitoba. Canadian Journal of Plant Science 41: 320-331.

Whalon, M. E. and B. L. Parker. 1978. Immunological identification of tarnished plant bug predators. Annals of the Entomological Society of America 71: 453-456.

Winder, L., J. N. Perry, and J. M. Holland. 1999. The spatial and temporal distribution of the grain aphid *Sitobion avenae* in winter wheat. Entomologia Experimetalis et Applicata 93: 277-290.

Winkler, K., F. Wackers, and D. M. Pinto. 2009. Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions. Ecological Entomology 34: 221–227.

Winkler, K., F. L. Wackers, A. J. Termorshuizin, J. C. van Lenteren. 2010. Assessing risk and benefits of floral supplements in conservation biological control. Biocontrol 55: 719-727.

Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. Biological Control 10: 4-15.

Wong G., M. Ngouajio, and K S. Charles. 2010. Brassica biofumigants improve onion and celery production systems. Journal of Sustainable Agriculture 34: 2-14.

Young, O. P. 1986. Host Plants of the Tarnished Plant Bug, Lygus lineolaris (Heteroptera: Miridae). Annals of the Entomological Society of America 79: 747-762.

Zandstra, B. H., T. A. Dudek, E. J. Grafius, M. L. Lacy, and D. D. Warncke. 1986. Commercial recommendations: celery. Michigan State University Extension Bulletin 1308.

Zandstra, B. H. 2012. Celery Weed Control Update. Great Lakes Fruit, Vegetable, & Farm Market Expo., Celery education session. Grand Rapids, MI.