

RELATIONSHIPS BETWEEN LANDSCAPE STRUCTURE, COCCINELLID ACTIVITY
DENSITY, AND APHID SUPPRESSION IN SOYBEAN

By

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ABSTRACT

RELATIONSHIPS BETWEEN LANDSCAPE STRUCTURE, COCCINELLID ACTIVITY DENSITY, AND APHID SUPPRESSION IN SOYBEAN

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Arthropod natural enemies provide valuable pest suppression in agricultural landscapes, and numerous studies have demonstrated the effects of landscape structure on natural enemy abundance and diversity. Coccinellid beetles are important generalist predators in a variety of agricultural landscapes, and have been found to be particularly important for suppression of the soybean aphid, *Aphis glycines*, Matsumura. I assessed the relationship between multiple landscape metrics and coccinellid abundances in soybean fields using Partial Least Squares regression. Coccinellid abundances were lowest in landscapes dominated by annual crops grown in large fields and highest in landscapes dominated by semi-natural habitat, with a higher diversity of crops grown in smaller fields. In addition to landscape-scale drivers, a large body of research examines the ability of local habitat management to enhance natural enemy efficacy. I examined the influence of landscape structure, local habitat management, and their potential interaction, on coccinellid abundances and *A. glycines* suppression in soybean. I selected pairs of soybean fields in landscapes of varying composition and planted buckwheat, *Fagopyrum esculentum*, strips adjacent to one field in each pair. *A. glycines* suppression was high in all contexts. Coccinellid abundance was higher in buckwheat than in control margins in all landscapes. Additionally, coccinellid abundance in soybean was positively related to amount of semi-natural vegetation in the landscape. I found no evidence of an interaction between

landscape and local variables, suggesting that landscape factors drive coccinellid potential to suppress soybean aphid.

Aphis glycines colonies are patchily distributed within soybean fields. To examine how coccinellid arrival rate at aphid-infested patches influences *A. glycines* control, I experimentally varied coccinellid immigration to 1m² soybean patches using selective barriers. In a year with low ambient aphid pressure, naturally-occurring levels of coccinellid immigration to host patches were sufficient to suppress aphid population growth. In contrast, *A. glycines* populations increased dramatically in patches with reduced coccinellid immigration. In a year with higher ambient aphid colonization, aphid suppression was incomplete. In a system in which natural enemy populations cannot track pest populations through reproduction alone, natural enemy immigration to infested patches can result in pest control. Finally, nocturnal predators have been shown to be responsible for significant predation of soybean herbivores in some regions, yet research on *A. glycines* natural enemies has focused on members of the diurnal predator community. I assessed diel variation of the predator community and *A. glycines* predation events. Anthocorids were responsible for the majority of observed predation, which occurred during daylight hours. Anthocorids and nabids were more active in the afternoon and carabids were more active at night. Different taxa were observed most frequently on video and within vacuum samples. Vacuum samples may represent predator abundance more accurately, while video data can be used to better assess relative time spent foraging. Overall, *A. glycines* population dynamics are influenced by a combination of local and landscape effects that structure predator communities and influence the spatial and temporal interactions between predators and this aphid. Factors that influence early season coccinellid immigration into infested patches show the greatest potential to improve *A. glycines* suppression.

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For Mama, who always wanted me to do whatever would make me happy, despite the fact that she would have found this whole process to be ridiculous.

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TABLE OF CONTENTS

LIST OF TABLES	xiii
LIST OF FIGURES	xvi
LITERATURE REVIEW	1
Introduction	1
Landscape effects on natural enemies and biocontrol services	3
Landscape composition	3
Seminatural habitats	3
Perennial crop habitats	4
Habitat and crop diversity	5
Landscape configuration	5
Differential responses by habitat generalists and specialists	6
Natural enemy prey specialization and immigration	7
Natural enemy dispersal ability and response to landscape	8
Local habitat effects on insect communities and biocontrol services	9
Habitat management	10
Interactions between landscape and local effects on natural enemies	11
Study system	12
Coccinellids and biological control of soybean aphid	14
Coccinellid responses to landscape and habitat management	15
Conclusions	16
LITERATURE CITED	18
CHAPTER I: Landscape structure and habitat management differentially influence coccinellids in an agricultural landscape	29
Abstract	29
Introduction	30
Methods	33
Site design	33
Buckwheat establishment and control margin characteristics	34
Aphid counts	34
Coccinellid counts	35
Biocontrol study	35
Landscape analysis	37
Statistical analysis	39
Coccinellid abundance	39
Biocontrol study	40
Results	40
Buckwheat establishment	40
Landscape analysis	41
Aphid counts	41
Coccinellid abundance	42

Biocontrol study	43
Discussion	44
Landscape effects on local management to improve services	44
Effects of local management on coccinellid beetles	45
Landscape effects on coccinellid beetles	46
Effects of predators on soybean aphid density	47
Conclusions	49
APPENDIX	51
LITERATURE CITED	74
 CHAPTER II: Coccinellid response to landscape structure across an agricultural intensification gradient.	80
Abstract	80
Introduction	80
Methods	84
Site design	84
Coccinellid counts	84
Landscape data	84
Measures of landscape composition	85
Abundance of primary land-covers	85
Cover diversity	85
Measures of landscape configuration	86
Crop mesh size	86
Landscape shape index	86
Statistical analysis	87
Results	89
Coccinellid captures	89
Landscape variables	90
PLSR model	90
Discussion	92
Conclusions	94
APPENDIX	96
LITERATURE CITED	101
 CHAPTER III: Coccinellid immigration to infested host patches influences suppression of <i>Aphis glycines</i> in soybean.	106
Abstract	106
Introduction	107
Methods	110
Site	110
Plot establishment	110
Predator monitoring	112
Aphid monitoring	113
Statistical analysis	114
Predator counts	114
Aphid abundance	115

Results	115
Adult coccinellid captures	115
Ground-dwelling predators	116
Foliar- and aerially-dispersing predators	118
Aphid abundance	118
Discussion	119
APPENDIX	124
LITERATURE CITED	135
 CHAPTER IV: Diel variation in natural enemy community of <i>Aphis glycines</i> in soybean	 140
Abstract	140
Introduction	140
Methods: Direct observation study	142
Study locations	142
Plot establishment	142
Aphid infestation	143
Aphid surveys	144
Predator sampling	144
Temperature	145
Statistical analysis	145
Aphid surveys	145
Vacuum samples	146
Methods: Video observation study	147
Study location	147
Aphid surveys	147
Video observations	147
Video processing	148
Statistical analysis	148
Aphid surveys	148
Vacuum samples	149
Video data	149
Results: Direct observation study	149
Colony establishment	149
Aphid surveys	149
Temperature	150
Predator observations	150
Vacuum samples	151
Results: Video observation study	151
Aphid surveys	151
Temperature	151
Vacuum samples	151
Video data	152
Discussion	152
Aphid colony establishment	152
Predator sampling method comparison	153
Use of video data in natural enemy surveys	155

APPENDIX	157
LITERATURE CITED	172
CHAPTER V: Conclusion	177
Implications for managing landscapes for ecosystem services	177
Context dependence of landscape effects	179
Expanding to underrepresented regions and agroecosystems	182
LITERATURE CITED	185

LIST OF TABLES

Table 1.1: Township, county and coordinates from soybean treatment and control fields used in 2008.	53
Table 1.2: Township, county and coordinates from soybean treatment and control fields used in 2009.	54
Table 1.3: Buckwheat strip data for 2008, including date each strip was planted and subsequently reached full bloom. Density (stems/10 cm ²) and height (cm) measurements were taken at full bloom.	55
Table 1.4: Buckwheat strip data for 2009, including date each strip was planted and subsequently reached full bloom. Density (stems/10 cm ²) and height (cm) measurements were taken at full bloom.	56
Table 1.5: Record of deposition of voucher specimens for Chapter I. The specimens listed below have been deposited in the Albert J. Cook Arthropod Research Collection, Michigan State University (MSU) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number 2013-08 have been attached or included in fluid preserved specimens.	57
Table 1.6: Dates soybean aphids were first detected in each treatment and control field, and dates cage study was conducted in each site in 2008.	58
Table 1.7: Dates soybean aphids were first detected in each treatment and control field, and date cage study was conducted in each site in 2009.	59
Table 1.8: A) Crop and B) non-crop land covers found in landscapes surrounding study fields. All land covers found were used to calculate Simpson's diversity metric (-lnD). The categories of grassland and forest land covers were subsequently combined into "semi-natural habitat" for landscape analyses.	60
Table 1.9: Simpson's diversity metric and proportion of each major land cover type surrounding study fields at the 2 km scale in 2008.	61
Table 1.10: Simpson's diversity metric and proportion of each major land cover type surrounding study fields at the 2 km scale in 2009.	63
Table 1.11: Effects of landscape and local habitat management on coccinellid abundance in 2008 soybean fields, 2009 soybean fields, and 2009 field margins. Separate analyses were run with A) Simpson's diversity index -lnD, and with B) proportion of semi-natural habitat in the landscape as the landscape descriptor variables. Results are shown for landscape values at the 2.0 km scale, but were consistent at all scales	65

Table 1.12: Mean $\pm$ S.E. of coccinellid beetles of each species found in soybean fields or field margins during 2008. No comparisons between treatment and control fields were significant in this year.	66
Table 1.13: Mean $\pm$ SE of coccinellid beetle species found in each field or field margin during 2009. Individual counts were rank transformed and compared using ANOVA. Asterisks (*) indicate a significant difference in abundance between buckwheat strips and control field margins, or between treatment and control fields (***) $p < 0.01$, ** $p < 0.05$, * $p < 0.1$).	67
Table 1.14: Biocontrol Services Index values for aphid suppression by natural enemies for each soybean field in 2008 and 2009.	68
Table 2.1: Landscape variables used in PLS analysis organized by variable type. Variables analyzed are shown in italics. Minimum and maximum values for each variable within the studied landscapes are shown, along with variable influence for project (VIP) values. Rx^2 indicates the amount of variation in each predictor variable explained by Factor 1.	98
Table 3.1: Means $\pm$ standard errors for all adult coccinellid species captured on sticky traps in 2010.	126
Table 3.2: Means $\pm$ standard errors for all adult coccinellid species captured on sticky traps in 2011.	127
Table 3.3: Means $\pm$ standard errors for the most common ground-dwelling predator species captured in pitfall traps in 2010 and 2011.	128
Table 3.4: Means $\pm$ standard errors for foliar-dispersing predators observed on soybean plants in 2010 and 2011.	129
Table 3.5: Means $\pm$ standard errors for aerially-dispersing predator species captured on sticky traps in 2010 and 2011.	130
Table 3.6: Average number of alate aphids observed per plant in each week in each plot in 2010 and 2011.	131
Table 4.1: Field locations and characteristics for direct and video observation of <i>A. glycines</i> predator communities and predation events.	159
Table 4.2: Record of deposition of voucher specimens for Chapter IV. The specimens listed below have been deposited in the Albert J. Cook Arthropod Research Collection, Michigan State University (MSU) museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number 2013-08 have been attached or included in fluid preserved specimens.	160

Table 4.3: Means $\pm$ S.E. of aphid change during each time period of the direct observation study. Bold indicates means that were significantly different from zero. Different letters indicate means which are significantly different from one another.	161
Table 4.4: Predators directly observed during 24 h aphid surveys. Observations were made 180 times at 0:00 and 3:00 h, and 360 times at all other time periods.	162
Table 4.5: Diel comparisons in predatory taxa from vacuum and video samples.	163
Table 4.6: Means $\pm$ S.E. of predators collected in vacuum samples of the direct observation study at morning (10:00), afternoon (16:00), and night (22:00).	164
Table 4.7: Means $\pm$ S.E. of aphid change during each time period of the video observation study. Means shown in bold are significantly different from zero. Different letters indicate means which are significantly different from one another.	165
Table 4.8: Means $\pm$ S.E. of predators collect in vacuum samples of the video observation samples at morning (9:00), afternoon (15:00) and night (0:00).	166
Table 4.9: Mean $\pm$ S.E. number of predator individuals observed in daylight hours during each three hour period of video surveillance.	167
Table 4.10: Mean $\pm$ S.E. number of predator individuals observed in night hours during each three hour period of video surveillance.	168

LIST OF FIGURES

Figure 1.1: Site locations of paired soybean fields across southern Michigan sampled for aphids and natural enemies in 2008 and 2009. Sites on the same or nearby farms from year to year appear to overlap at this scale (crossed circles), but samples were collected in a different set of fields in each year. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation. 69

Figure 1.2: Schematic of sampling design showing relative locations of plots and buckwheat strip or control field margin. Inset: a yellow sticky trap and a pair of caged and uncaged soybean plants for the biocontrol experiment were located in the center of each plot. 70

Figure 1.3: An example buckwheat strip in full bloom in July 2009. 71

Figure 1.4: **A)** Coccinellid abundance in field margins was consistently and significantly higher in buckwheat strips than in control field margins across a gradient of semi-natural habitat within landscapes. **B)** Coccinellid abundance in soybean fields in 2009 increased significantly with the proportion of seminatural habitat in the surrounding landscape at 2.0 km. The effect did not differ between fields adjacent to or without buckwheat strips. 72

Figure 1.5: Average number of aphids per soybean plant exposed to and excluding predators in treatment and control fields, at 7 and 14 days after infestation in **A)** 2008 and **B)** 2009. The horizontal dashed line indicates the economic threshold for soybean aphid of 250 aphids/ plant. In both years, natural enemies dramatically suppressed soybean aphid populations, and the differences in aphid populations between caged and uncaged plants were greater at 14 days than at 7 days. However, buckwheat treatment did not significantly affect the size of the difference in aphid populations on caged and uncaged plants in either year. 73

Figure 2.1: Relationship between coccinellid abundance in soybean fields in 2009 and landscape variable scores from PLS analysis. Predictor and explanatory variables show a positive correlation within factor 1, suggesting that this factor captures a real relationship between these variables. 99

Figure 2.2: Loadings of response (coccinellids, in box) and predictor (landscape) variables from PLS regression. The abundance of coccinellids loads positively along factor one, along with non-crop habitats like *grasslands*, *residential areas*, and *forests*, and with crop diversity (SDI_{crop}). In contrast, annual crops (*maize*, *soybean*, *wheat*) and crop field size (*MESH*) load negatively. The numbers 1 through 17, representing the landscapes, are generally spread-out and show no obvious outliers. 100

Figure 3.1: Predator activity-density and aphid abundance were measured in 1 m^2 plots. Barriers to coccinellid immigration were constructed with 2 mm opening mesh netting and were raised 2 cm above the ground to allow full access by small and ground-dwelling

predators. Open plots (A & D) had no barriers to immigration. 2-sided plots (B & E) had barriers erected on the east and west sides of plot. 5-sided plots (C & F) had barriers on all sides. Each field contained two sets of plots. In sampling plots (A-C), predators were sampled without replacement. In observation plots (D-F), aphid populations were monitored without disturbing predator populations. 132

Figure 3.2: Mean number of adult coccinellids captured in treatment plots in 2010 and 2011. In 2010, coccinellid immigration was higher in open and 2-sided than in 5-sided treatment plots. In 2011, coccinellid immigration rates were different in all treatments. 133

Figure 3.3: Mean number of *A. glycines* observed per plant each week in soybean fields outside of plots and in open, 2- and 5-sided treatment plots in 2010 and 2011. Symbols indicate significantly more aphids in (+) 5-sided and 2-sided than in open plots, (*) between all treatments and (x) in 5-sided than in open or 2-sided plots. 134

Figure 4.1: Diagram of plot set-up for observation study. A) Two exterior plots were situated from 0 – 10 m into the field. B) Two interior plots were situated from 50 – 60 m into the field. All plots were 50 m away from all other field edges. C) Expanded view of plot demonstrated random selection of plants for aphid infestation. D) Caged plants located in between plots were used to account for mortality in the absence of predation. 169

Figure 4.2: Video observation set-up. A) Aphids were recorded with video surveillance cameras suspended from PVC frames. B) 8 cameras were arranged radially around a DVR. C) The DVR was powered by 2 marine batteries and connected to a removable hard drive rack that allowed video files to be taken to the lab for uploading and viewing. 170

Figure 4.3: The percentage of plants on which aphid colonies decreased, remained steady, or increased within 6 h of infestation. Plants were infested prior to dusk or dawn and were caged to exclude predators or uncaged to be exposed to predators. 171

LITERATURE REVIEW

Introduction

Agricultural landscapes cover at least one quarter of terrestrial surfaces on our planet (Millennium Ecosystem Assessment, 2005) and are critical for providing food, fuel and fiber for our growing global population. In addition to these provisioning services, agricultural landscapes also contribute to supporting, regulating and cultural services. For example, agricultural landscapes can be managed to support the biodiversity that underpins many ecosystem services, as well as the regulation of water quality, soil fertility, and greenhouse gases (Swinton et al. 2007, Power 2010). They can also be managed to minimize disservices like soil and nutrient runoff and exposure to pesticides (Power, 2010). By altering the interactions of the organisms that live there, landscape structure, including the identity, relative abundance, and arrangement of various habitat types, affects ecosystem functions and thus the provision of ecosystem services in agricultural landscapes (Altieri 1999, Schlapfer et al. 1999, Tilman et al. 2002, Kremen 2005). As such, understanding how to best manage these landscapes to provide a sustainable supply of these ecosystem services is critical.

Within agricultural landscapes, insects provide vital ecosystem services like pollination, decomposition and biological control of crop pests by predator and parasitoid natural enemies (Losey and Vaughan 2006). These insect communities, and thus the services they provide, are also influenced by the landscape context. For example, landscape structure affects the composition of insect communities and the abundance of individual species, which in turn influences biocontrol (Tscharntke et al. 2005). Local habitats, or those adjacent to crop fields, can also affect insect communities and biocontrol services in their vicinity. Herbaceous and woody vegetation adjacent to crop fields provide resources to natural enemies, contributing to

population increases and greater pest control (Bianchi et al. 2006). In many cases, local habitat can be manipulated to provide natural enemies with resources like alternative prey and refuge habitat to optimize their performance, a practice known as habitat management (Landis et al. 2000).

Because landscape structure affects insect communities at a variety of scales, the ability of habitat management to improve biocontrol services can be expected to depend on landscape complexity and composition. Tscharntke et al. (2005) found that local management practices only had an impact on biocontrol services in simplified landscapes, presumably because complex landscapes already supply natural enemies with necessary resources. On the other hand, extremely simplified landscapes may not support sufficient natural enemy populations to measure significant effects of habitat management. Furthermore, natural enemies may respond to multiple aspects of landscape structure, including heterogeneity of semi-natural areas, heterogeneity of crop habitats, and the configuration or spatial arrangement of land covers (Fahrig et al. 2011). Additionally, the diversity of agronomic practices (e.g. forms of tillage, fertilization regimes and pesticide usage, timing of practices) can create environments with different suitability for natural enemies in multiple fields of the same crop type (Vasseur et al. 2013). However, in spite of the complexity of possible interactions between natural enemies and landscape structure, studies examining these effects routinely characterize landscapes solely by the amount of semi-natural habitat present (Burel et al. 2013). In light of the fact that farmers are likely to be more willing and able to manage some aspects of landscape structure (like crop heterogeneity) than others (like natural areas), a more detailed examination of the interaction between landscape structure and insect communities could lead to more practical management recommendations (Fahrig et al. 2011). Finally, in addition to community effects, landscapes

could influence the timing and degree of natural enemy dispersal (Bianchi and van der Werf 2003), which could have implications for pest suppression in agroecosystems (Landis and van der Werf 1997).

Landscape effects on natural enemies and biocontrol services

Agricultural landscapes exist as a mosaic of crop and non-crop habitats, which organisms may use in a variety of ways (Fahrig et al. 2011). Landscape structure itself can be quantified in multiple ways, including composition metrics that describe which and how many habitats are present and their relative abundances, and configuration metrics that indicate how those habitats are spatially arranged (Turner et al. 2001). Cummings and Spiesman (2006) point out the importance of understanding the effects of landscape structure on ecosystem services like pest management. Natural enemies are thought to control most potential crop pests much of the time (Losey and Vaughan 2006), yet the success of biological control is dependent upon the provision of natural enemies by the landscape. Landscape structure could impact the success of biocontrol by affecting the ability of natural enemies to locate and aggregate in areas of high pest density (Bommarco 1998).

Landscape composition. *Semi-natural habitats.* Non-crop habitats like forests and grasslands can play an important role in agricultural landscapes by providing natural enemies with food sources like nectar, pollen, and prey (Thies et al. 2003), as well as refuge from insecticide use (Lee et al. 2001), tillage, and harvest (Landis et al. 2000). Having access to these resources can lead to increased populations of natural enemies like coccinellids (Coleoptera: Coccinellidae) (Gardiner et al. 2009a), spiders (Araneae) (Schmidt and Tscharntke 2005, Drapela et al. 2008, Gardiner et al. 2010, Pluess et al. 2010), carabids (Coleoptera: Carabidae) (Purtauf et al. 2005, Batáry et al. 2007), and Opiliones (Prasifka et al. 2004, Gardiner et al. 2010). These

perennial non-crop habitats can also support higher species richness of many natural enemy taxa, including spiders (Clough et al. 2005, Schmidt et al. 2005, Drapela et al. 2008, Schmidt et al. 2008), coccinellids (Colunga-Garcia et al. 1997), and carabids (Purtauf et al. 2005, Batáry et al. 2007, Werling and Gratton 2008). The increases in natural enemy abundance and richness in landscapes with more semi-natural habitat may contribute to better control of crop pests, as these landscapes have also been found to have higher suppression rates of rape pollen beetle, *Meligethes aeneus* (F.) (Coleoptera: Nitidulidae) (Thies and Tscharnke 1999, Thies et al. 2003), cabbage moth, *Mamestra brassicae* L. (Lepidoptera: Noctuidae) (Bianchi et al. 2005), cereal aphids (Hemiptera: Aphididae), *Sitobion avenae* (F.), *Metopolophium dirhodum* (Walker), and *Rhopalosiphum padi* (L.), (Roschewitz et al. 2005, Thies et al. 2005), diamond back moth, *Plutella xylostella* (Lepidoptera; Plutellidae) (Bianchi et al. 2008), and soybean aphid, *Aphis glycines* Matsumura (Gardiner et al. 2009a). In fact, a meta-analysis of landscape studies showed that natural enemy activity was enhanced by landscape heterogeneity in 70% of cases, and landscape composition measured as proportion of woody and herbaceous habitat in 71% and 80% of cases, respectively (Bianchi et al. 2006).

Perennial crop habitats. Studies of landscape composition effects on insects typically consider only semi-natural habitats (Burel et al. 2013). However, other types of land covers could also influence natural enemy communities. For example, perennial crops may provide many of the same benefits as semi-natural habitat, including reduced disturbance and alternative prey (Landis et al. 2000). Although studies examining perennial crops have been few in number, landscapes which contain more perennial crops have been found to have higher natural enemy activity density (Oberg et al. 2007) and diversity (Elliott et al. 1999), and lower pest rates (Östman et al. 2001). Additionally, natural enemies may have higher fitness and fecundity in

landscapes with more perennial crops (Bommarco 1998). Perennial crops may also allow populations of natural enemies to persist year to year due to their lower levels of disturbance (Landis et al. 2000).

Habitat and crop diversity. Habitat diversity, another metric of landscape composition (Turner et al. 2001, McGarigal et al. 2012), may also be important for naturally occurring biological control. Multiple land covers in a local area may provide different resources needed by a single organism (Dunning et al. 1992), which can in turn influence communities in agricultural landscapes (Fahrig et al. 2011). For example, a predatory insect may require one type of habitat for overwintering and another for foraging and egg-laying. High habitat diversity in the landscape can also support greater predator density by allowing cross-foraging (Cumming and Spiesman 2006). Predators receiving prey “subsidies” from other habitats may increase in abundance and more effectively suppress pests in focal areas (e.g. crop fields) (Polis et al. 1997). Additionally, because different habitat types support different natural enemies, landscapes with higher habitat diversity may support higher natural enemy diversity (Elliott et al. 1999, Bianchi et al. 2006), which can facilitate recovery of pest suppression services after disturbances (Tscharntke et al. 2005). Conversely, simplified landscapes of predominantly crop land support lower biodiversity (Bianchi et al. 2006), and may lead to a loss of ecosystem services like pest control (Andow 1983, Kareiva 1987, Thies and Tscharntke 1999, Symondson et al. 2002, Tscharntke et al. 2005). Crop diversity may provide many of the same benefits as overall habitat diversity, as different crops with different phenologies may provide complementary resources at different times of the year (Vasseur et al. 2013).

Landscape configuration. In contrast to measures of landscape composition, the influence of landscape configuration on natural enemies has been largely overlooked (Burel et al.

2013). Yet the configuration of habitats can affect the rate of arrival of natural enemies into crop fields (Bianchi et al. 2006), which can in turn influence natural enemy efficacy (Hogg and Daane 2010). In particular, modeling has shown that an even distribution of non-crop habitats within a landscape should facilitate colonization of fields by natural enemies (Bianchi and van der Werf 2003), suggesting that landscapes with small crop fields and greater dispersion of non-crop habitat could promote higher natural enemy abundances in crop fields. Additionally, researchers have found greater pest control in small fields adjacent to larger non-crop borders than in larger fields with less border area (Marino and Landis 1996, Werling and Gratton 2010). Furthermore, landscapes with smaller average patch sizes should promote early colonization of crop fields by natural enemies (Bianchi et al. 2009), which could lead to higher biocontrol in landscapes with smaller patch size (Bianchi et al. 2006).

Differential responses by habitat generalists and specialists

A natural enemy taxon's degree of habitat specialization affects how it will perceive and be influenced by the landscape. Habitat specialists may require a high degree of landscape diversity to fulfill their needs, while generalists may be more dependent on overall area of appropriate habitat (Ricklefs and Lovette 1999). Landscapes may appear more fragmented to specialized species, which require resources from specific habitat types, and more connected for generalists because they are able to use more of the habitat types on the landscape (Kruess and Tscharntke 1994, Tscharntke et al. 2002). Alternately, landscape heterogeneity may be important to habitat generalists due to provision of diverse resources, while habitat specialists depend more on connectivity and total area of specific habitat types (Steffan-Dewenter 2003).

Natural enemy prey specialization and immigration

In addition to variation in habitat specialization, natural enemies of crop pests also exhibit a wide range of prey specificity. Modeling studies suggest that effective pest suppression may be obtained from either specialist natural enemies inflicting high mortality rates, or from generalist natural enemies with high immigration rates into an infested area (Chang and Kareiva 1999). Additionally, each of these strategies may be better adapted to particular crop types. For example, specialist natural enemies may be well-adapted for perennial crops in which temporal stability allows equilibrium to be achieved between natural enemy and pest populations, while generalists may be better suited for annual crops which both pests and natural enemies have to recolonize each growing season (Murdoch et al. 2006). Furthermore, because generalist natural enemies like coccinellids tend to have long generation times relative to those of their prey and thus cannot rapidly respond numerically to pest population dynamics (Dixon et al. 1997, Kindlmann and Dixon 1999b, a, 2001), generalists must exhibit high immigration rates to be effective (Murdoch et al. 2006). In fact, higher immigration rates have been demonstrated to decrease the predator/prey ratios necessary for effective pest suppression (van der Werf 1995), and manipulating immigration rates of generalist predators has resulted in lower pest abundance and higher yields (Snyder and Wise 1999).

Natural enemy immigration occurs at different temporal and spatial scales. In annual agriculture, many natural enemies overwinter outside of the crop and must first immigrate into crop fields after their establishment. Once in the crop habitat, they must then disperse and locate prey-infested patches within the field. In situations in which natural enemies must immigrate into fields, the timing of immigration is important for pest suppression. Natural enemies must arrive prior to pest populations reaching high densities and growing exponentially. Reducing natural

enemies in the early season or preventing them from colonizing pest-infested patches can result in higher pest densities later in the season (Settle et al. 1996, Landis and van der Werf 1997).

Natural enemy dispersal ability and response to landscape

Dispersal ability influences the scale at which landscape structure influences insect communities and individual insect success (Roland and Taylor 1997, Bommarco 1998). Habitat connectivity is less important for vagile species than for poor dispersers, with the result being that landscapes appear more fragmented to poor dispersers (deVries et al. 1996, Tschamntke et al. 2002). For example, in a study of coccinellid ability to track aphid populations in fragmented landscapes, distributions of the native coccinellid *Coleomegilla maculata* (DeGeer) were more affected by habitat fragmentation than those of the exotic coccinellid *Harmonia axyridis* (Pallas), which is a better disperser (With et al. 2002). Several studies have estimated the spatial scale at which particular insects respond to landscape features by first quantifying the landscape composition at various radii around a study plot and then determining the scale at which landscape composition and insect density was most highly correlated (Steffan-Dewenter et al. 2001, Steffan-Dewenter et al. 2002, Krauss et al. 2003, Thies et al. 2003, Westphal et al. 2003, Drapela et al. 2008, Pluess et al. 2010). These studies have shown different scales of response for different types of insects. Overall, natural enemy diversity and abundance and pest suppression have been related to the structure of the surrounding landscape at scales between hundreds of meters to 10 km (Woltz et al. 2012). Because dispersal ability of insects affects the scale at which they respond to landscape structure, parasitoids with small dispersal ranges are expected to respond at smaller scales, while generalist predators like beetles are affected at larger scales (Tschamntke et al. 2005). Even among coccinellids, the different life histories and dispersal abilities of various species cause them to respond to landscape features at different scales,

although, in general, landscape factors have greater impacts than within field variables on coccinellid abundance and diversity (Elliott et al. 1998). Finally, the dispersal abilities of different natural enemy taxa determine which species coexist in crop fields (Bianchi et al. 2009). Therefore, natural enemy responses to landscape structure are primarily driven by highly mobile taxa (Tscharntke et al. 2005).

Local habitat effects on insect communities and biocontrol services

Local habitat characteristics, those of the crop field of interest and its immediate surroundings, also affect insect communities in agro-ecosystems. Natural enemies have several requirements, including appropriate microclimates, constant food supplies, and overwintering habitats (Jonsson et al. 2008) that are not continuously available in crop habitats. Crop fields are frequently disturbed by tillage, planting, pesticide application, and harvest, making them temporarily unsuitable for natural enemies to inhabit (Landis et al. 2000). Thus, the suitability of adjacent habitats for natural enemies affects their ability to survive crop disturbances and recolonize crop fields. Insects, including natural enemies of crop pests, often survive in field edges and non-crop habitats such as woodlots and hedgerows during crop disturbance (Duelli et al. 1999, Bianchi et al. 2006). Natural enemies also overwinter in nearby non-crop habitat, from which they subsequently recolonize crops during the growing season (Bianchi et al. 2006, Benjamin et al. 2008). Herbaceous habitats may provide especially important overwintering habitats for generalist predators (Geiger et al. 2009). Local non-crop habitat can also provide nutritional resources for natural enemies. Herbaceous and woody vegetation adjacent to crop fields can support alternative hosts for parasitoids and prey for predators, as well as nectar and pollen sources (Meek et al. 2002). The presence of alternate prey may allow natural enemies to

establish before populations of pests do so (Landis et al. 2000), providing greater pest control (Bianchi et al. 2006).

Habitat management

Conservation biological control refers to practices aimed at increasing the effectiveness of natural enemies already present in the landscape (Landis et al. 2000). Habitat management is a type of conservation biological control that involves altering habitats within or adjacent to crops to provide natural enemies with resources necessary to optimize their performance (Landis et al. 2000). Such resources could include alternative prey or hosts (Settle et al. 1996), nectar and pollen (Treacy et al. 1987, Idris and Grafius 1995, Hickman and Wratten 1996), overwintering habitat (Thomas et al. 1992), and refuge from field disturbances (Landis et al. 2000).

Habitat management often involves increasing the diversity of plants within an agroecosystem, whether within a field, along a crop border, or in the broader landscape (Gurr et al. 2003). The use of field borders for habitat management often takes the form of linear strips such as beetle banks or floral resource strips. Floral resource strips are used to increase insect diversity and to support pollinators and natural enemies of crop pests (Haaland et al. 2011). Floral plantings may increase natural enemy efficacy by providing them with resources such as nectar, pollen, or alternative prey (Landis et al. 2000). For generalist predators that are less reliant on floral resources, the vegetative structure of plantings can be important (Haaland et al. 2011), and grassy strips may shelter greater abundances than adjacent fields (Smith et al. 2008). Vegetation strips can serve as a refuge from crop disturbance allowing natural enemies to recolonize fields after insecticide application (Lee et al. 2001). Moderated microclimate and carbohydrate resources can increase parasitoid longevity, resulting in greater lifetime parasitism rates (Costamagna and Landis 2004). However, in some cases, field margin plantings may harbor

natural enemies, but not result in higher natural enemy densities within the adjacent crop (Koji et al. 2007).

In general, floral plantings support higher abundances of natural enemies than crop edges or fields (Haaland et al. 2011). Non-crop flowers can increase abundance of ground-dwelling generalist predators like spiders and carabid beetles (Ditner et al. 2013) probably by providing more favorable microclimates. Floral resource strips have been shown to result in higher abundances of beneficial insects (Walton and Isaacs 2011), higher aphid parasitism rates (Bigger and Chaney 1998, Langer and Hance 2004), greater egg-laying by syrphids and lower aphid densities (Hickman and Wratten 1996), and higher pest predation rates (Frank and Shrewsbury 2004) in adjacent crop fields. However, not all natural enemy taxa respond in the same way, and some that are found in great abundance in the strips are less abundant in adjacent crops (Bigger and Chaney 1998). Additionally, effects may be idiosyncratic, impacting some pests but not others, or working in some sites but not others (Pfiffner et al. 2009).

Interaction between landscape and local effects on natural enemies

Non-crop habitats, provided locally within the landscape, provide important resources for natural enemies, yet the natural enemies that respond to local resources ultimately come from the broader landscape. Clough et al. (2007) concluded that “the landscape determines potential insect diversity that may be realized or not depending on local conditions.” This can create complicated dynamics between landscape and local effects on natural enemies. Landscape structure has been shown to have more influence on natural enemy communities than local adjacent habitats in cotton (Prasifka et al. 2004) and potatoes (Werling and Gratton 2008), although Werling and colleagues (2010) found that both landscape conditions and local adjacent habitats influenced pest predation in potato fields. Others have simultaneously examined the

impact of landscape structure and conventional vs. organic management. In some cases, landscape characteristics have been shown to have greater influences on natural enemies than field management (Clough et al. 2005, Purtauf et al. 2005), while in others, both landscape and field management influenced natural enemies (Schmidt et al. 2005, Isaia et al. 2006), and pests (Östman et al. 2001, Roschewitz et al. 2005). In some cases, landscape structure is even more influential on natural enemy communities than the particular habitat in which natural enemies are sampled (Aviron et al. 2005) while others saw influences of both (Wilby et al. 2006).

Together, these studies suggest that while in some systems landscape factors are overriding, in others both scales may simultaneously influence natural enemies. In some cases, landscape and local effects may even be interactive. For example, Haenke and others (Haenke et al. 2009) found that syrphid densities were higher in flower strips than in grassy strips, but within flower strips syrphid densities also increased with amount of crop in the landscape, perhaps suggesting that the syrphids aggregated in the flower strips in the more resource-poor landscapes. Conversely, others have found that spider density (Schmidt et al. 2005) and carabid richness (Weibull et al. 2003) were related to landscape conditions in conventional but not organic farms, indicating that landscape conditions were more important for natural enemies on resource-poor farms.

Study System

Soybean, *Glycine max*, is an ideal system to compare the effects of landscape complexity and local habitat management on biocontrol services because it is attacked by a common insect pest which is in turn preyed upon by a diverse guild of broadly occurring generalist predators (Ragsdale et al. 2004, Costamagna and Landis 2007). Aphids are common crop pests world-wide, feeding on crops as diverse as limes, cabbage, and beans (Dixon 1985). Soybean aphid,

Aphis glycines Matsumura, specializes on soybean, causing heavy damage (Wu et al. 2004).

Soybean aphid natural enemy abundance is correlated with landscape features (Gardiner et al. 2009a) and may respond to floral resources (Harmon et al. 2000).

Aphis glycines was first detected in the U.S. in Wisconsin in July 2000 (Ragsdale et al. 2004) and has since been reported in 22 states and 3 Canadian provinces (Costamagna and Landis 2007). Aphids are dispersed long distances by wind, and may ultimately spread into most soybean production areas of the U.S. (Venette and Ragsdale 2004). *Aphis glycines* exhibits a heteroecious, holocyclic life cycle, overwintering on *Rhamnus* sp., and emigrating to soybean in early spring (Ragsdale et al. 2004), where it causes yield losses of up to 40% in the North Central US (DiFonzo and Hines 2002). Heavy infestations may result in early defoliation, shortened stems and leaves, underdeveloped roots, distorted foliage, reduced branch number, lower seed and pod counts, reduced seed weight, and stunting (Wu et al. 2004). In the North Central U.S. soybean was rarely sprayed with insecticide before *A. glycines* arrival; however, soybean aphid presence has led to increased pesticide use, with 2.8 million ha sprayed in the North Central U.S. in 2003 (Landis et al. 2003). Soybean aphid can be a vector of crop viruses, including soybean mosaic virus, soybean dwarf virus, soybean stunt virus, and several others (Heimpel et al. 2004, Wu et al. 2004). *Aphis glycines* could negatively affect native aphids and other herbivores through direct or apparent competition (Heimpel et al. 2004). Soybean aphid abundances may have driven increases in populations of exotic coccinellids, leading to the displacement of native species (Heimpel et al. 2004).

Factors such as natural enemy abundance, timing of soybean field invasion, temperature, and moisture may impact soybean aphid outbreaks. For example, wetter and cooler weather favors soybean aphid population growth (Ragsdale et al. 2004). In the North Central U.S.

maximum daily temperatures in June are often 22-25 °C, temperatures which favor rapid soybean aphid development (Ragsdale et al. 2004). Outbreaks of soybean aphids are mediated by the number of overwintering eggs, synchronization of aphid and soybean development, and crop management practices including sowing time and crop rotation (Wu et al. 2004).

Coccinellids and biological control of soybean aphid. Effective biocontrol of *A. glycines* could reduce economic and environmental costs associated with insecticide application if pests are kept below economic injury thresholds (Heimpel et al. 2004). Ragsdale et al. (2007) estimated an economic threshold (ET) of 273 ± 38 soybean aphids per plant, with a seven day lead time before populations would be expected to exceed the Economic Injury Level (EIL) of 674 ± 95 aphids per plant. In order to effectively suppress soybean aphid, natural enemies must attack early in the season when aphid populations exhibit low density and slow growth (Wu et al. 2004), or aggregate in areas of high aphid density later in the season, and have high attack rates (Rutledge et al. 2004). Generalist predators have been shown to suppress *A. glycines* during both early season aphid establishment and mid-season aphid population increase (Costamagna and Landis 2006). In particular, coccinellids occur early in the season and in sufficient numbers to potentially prevent outbreaks (Rutledge et al. 2004). Coccinellid beetles are thought to contribute the greatest amount to control of this pest in China (Wu et al. 2004). In an observational study of the soybean aphid predator guild, adults and larvae of large coccinellid species such as *Coccinella septempunctata* and *Harmonia axyridis* accounted for a majority of soybean aphid predation (Costamagna and Landis 2007). These species had the highest per capita consumption rate of *A. glycines*, consumed aphids rapidly, and increased in abundance and predation rate in response to increased soybean aphid density. Coccinellids in general have been shown to efficiently control soybean aphid populations, leading to significant increases in plant biomass

and soybean yield (Costamagna and Landis 2007). *Harmonia axyridis* acts to reduce aphid densities, arriving early in the season before aphids, and responding numerically to aphid abundances (Rutledge et al. 2004). Additionally, intraguild predation by large coccinellids has been shown not to release soybean aphid from biological control, as *H. axyridis* supplies sufficient control to make up for lost intermediate predators (Costamagna and Landis 2007, Gardiner and Landis 2007). Furthermore, Costamagna and Landis (2007) did not observe intraguild predation during the course of their observational study and recorded very few predation events on alternate prey, indicating that soybean aphid is a primary prey item for coccinellids in soybean fields.

Coccinellid responses to landscape and habitat management. An abundance of evidence suggests that coccinellids respond to both local and landscape conditions. Coccinellids have been found to be more abundant within habitat management strips themselves (Dong et al. 2012), and also more abundant in vineyards with adjacent noncrop habitat than in vineyards without such adjacent habitats (Thomson and Hoffmann 2010). Additionally, the increased abundances of coccinellids and other predators lead to higher predation rates of pest eggs in the vineyards with adjacent noncrop vegetation (Thomson and Hoffmann 2010), suggesting that habitat management can be a useful tool for improving biocontrol services from coccinellids. At larger scales, coccinellids are highly responsive to landscape composition in agroecosystems (Colunga-Garcia et al. 1997, Elliott et al. 2002, Gardiner et al. 2009a), although specific responses may differ by species (Colunga-Garcia et al. 1997, Gardiner et al. 2009b). Furthermore, the response of coccinellids to landscape structure has been related to greater suppression of *A. glycines* in landscapes with more diverse non-crop habitat (Gardiner et al. 2009a). Such evidence of coccinellid response to both habitat management and landscape

structure, and the related implications for pest suppression at both scales, suggests a need to compare effects at these two scales simultaneously and to consider possible interactions between them. However, because studies have shown contrasting responses of coccinellids to overall abundance of crop and non-crop habitat in a landscape (Gardiner et al. 2009a, Caballero-Lopez et al. 2012), it is necessary to begin examining coccinellid's relationship to landscape structure in more detail. Additionally, coccinellid immigration and resulting densities at a patch level are influenced by small-scale fragmentation, as well as patch isolation (Grez et al. 2004, Grez et al. 2005, Zaviezo et al. 2006). These influences on the aggregation behavior of coccinellids could influence aphid outbreaks (Kareiva 1987), suggesting a need to examine the relationship between coccinellid immigration and soybean aphid suppression.

Conclusions

The occurrence of natural enemy communities that provide biocontrol services within agroecosystems is dependent upon landscape characteristics. Biocontrol services can also be augmented with habitat management practices that provide natural enemies with additional food and habitat resources to natural enemies. It is unknown, however, whether landscape structure and habitat management interact, such that habitat management practices improve biocontrol services more in certain types of landscapes than in others. Highly diverse landscapes may already provide a sufficient supply of natural enemies for biocontrol, while extremely simplified landscapes likely support few natural enemies to respond to additional resources (Tscharntke et al. 2005). Furthermore, multiple aspects of landscape structure are relevant for natural enemy communities, while prior studies have typically focused on a single aspect of landscape composition. Finally, because landscape structure may influence natural enemy dispersal as well

as abundance, it is important to understand how changes in natural enemy dispersal could influence pest suppression.

The objectives of this dissertation are to: 1) examine the effectiveness of habitat management for soybean aphid biological control in landscapes of varying complexity, 2) to examine in detail specific aspects of landscape structure that influence coccinellid abundances, 3) to examine the influence of coccinellid immigration on soybean aphid suppression, and 4) to compare diel patterns in the soybean aphid natural enemy community.

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CHAPTER I: Landscape structure and habitat management differentially influence coccinellids in an agricultural landscape

Abstract

Woltz, J.M., R. Isaacs, and D.A. Landis, 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. *Agriculture, Ecosystems, and Environment* 152: 40-49.

Increasing evidence suggests that landscape composition is an important driver of beneficial insect populations and resulting ecosystem services. Additionally, local-scale manipulations such as planting floral strips are used at the field-level to provide resources for beneficial insects to increase their services. It has been proposed that the benefits of local manipulations will depend on the landscape context, with greater benefits in simplified landscapes and smaller benefits in landscapes with an abundance of non-crop resources. To test this, we used soybean aphid, *Aphis glycines*, and its coccinellid predators as a model system to elucidate the effects of habitat management and landscape on biocontrol services in soybean. We selected pairs of soybean fields in landscapes of varying composition and planted buckwheat, *Fagopyrum esculentum*, strips adjacent to one field in each pair. We measured coccinellid abundance and biocontrol in each field. Coccinellid abundance was higher in buckwheat than in control field margins in all landscapes, and coccinellid abundance in soybean was positively related to amount of semi-natural vegetation in the landscape. We found no evidence of an interaction between landscape and local variables, and biocontrol services were high in all contexts. For soybean aphid suppression, landscape factors are the key drivers of predator abundance.

Introduction

Landscape complexity and local management of agricultural lands can influence the diversity of plants, animals, and microorganisms (Altieri 1999, Tscharntke *et al.* 2005) which in turn affect the provision of ecosystem services such as nutrient cycling, water regulation, and pest suppression provided by beneficial insects (Altieri, 1999; Schlapfer *et al.*, 1999; Tilman *et al.*, 2002; Kremen, 2005). Biological control of crop pests is an ecosystem service valued at US\$ 4.5 billion/yr in the United States alone (Losey and Vaughan, 2006), and it can reduce the need for costly chemical pesticides and associated environmental and human health concerns (Meehan *et al.*, 2011). In order to support this valuable ecosystem service, various on-farm management practices have been developed to increase natural enemy diversity and abundance. For example, planting non-crop habitats adjacent to crop fields can provide natural enemies with additional food resources and refuge from disturbance (Landis *et al.* 2000), and may decrease the negative impacts of farming on local biodiversity (Concepción *et al.* 2008). However, recent studies demonstrating the influence of landscape-scale factors on biocontrol services have led some to hypothesize that the landscape context may constrain the ability of local management actions to influence community dynamics and biocontrol services (Concepción *et al.* 2008, Tscharntke *et al.* 2012).

Landscape composition influences natural enemy communities through the provision of food and shelter resources. Complex landscapes with large amounts of semi-natural habitat may benefit natural enemies by providing undisturbed areas that offer shelter from crop disturbances, overwintering refuges, alternative hosts and prey, and additional nectar resources (Thies *et al.*, 2003; Bianchi *et al.*, 2006). As such, the amount of non-crop or semi-natural habitat in a landscape has been positively related to the abundance of a variety of predators, including

spiders (Drapela *et al.*, 2008; Schmidt *et al.*, 2008), carabid beetles (Purtauf *et al.*, 2005), coccinellid beetles (Gardiner *et al.*, 2009), and opiliones (Gardiner *et al.*, 2010). A meta-analysis of 46 landscape-scale studies in agroecosystems showed positive relationships between the amount of natural or non-crop habitat in the landscape and natural enemy abundance and diversity, predation and parasitism (Chaplin-Kremer *et al.* 2011).

Landscape-mediated increases in natural enemy abundance and diversity can in turn lead to higher predation and parasitism rates, and thus greater pest control. Thies and Tscharntke (1999) found that high rates of plant damage by the rape pollen beetle, *Meligethes aeneus* (Fabricius), and low rates of parasitism and larval mortality were correlated with landscape simplicity, while parasitism by two key parasitoid species increased with landscape heterogeneity. In a study by Gardiner *et al.* (2009), biocontrol of soybean aphid, *Aphis glycines* Matsumura, was greater in diverse compared to agriculturally dominated landscapes, and in landscapes with greater amounts of non-crop habitat. Similarly, the percentage of non-crop area in the landscape has been positively related to parasitism-induced mortality of true armyworm *Pseudaleta unipuncta* (Haworth) (Marino and Landis, 1996) and negatively related to pest damage by rape pollen beetles (Thies *et al.*, 2003).

At the field or farm scale, local habitat can also be manipulated to provide natural enemies with resources to optimize their performance, a practice known as habitat management (Landis *et al.*, 2000). Floral resource strips are commonly used to increase natural enemy efficacy by providing them with resources such as nectar, pollen, or alternative prey (Landis *et al.*, 2000). Efforts to increase biocontrol with floral strips have met with mixed success, with some studies showing no effect on predator abundance within fields (Bigger and Chaney, 1998; Koji *et al.*, 2007) and others leading to increased predator or parasitoid abundance and reduced

pest pressure in crop fields (Hickman and Wratten, 1996; Langer and Hance, 2004; Lee and Heimpel, 2005). Because the surrounding landscape supplies the natural enemies that may respond to floral resource strips, it is possible that the ability of habitat management to influence pest control depends on the landscape context in which a particular crop field is situated. Tscharrntke *et al.* (2005) suggested that local management practices may only increase biocontrol services in partially simplified landscapes, presumably because complex landscapes already supply natural enemies with necessary resources, while landscapes almost entirely cleared for agriculture may not support sufficient natural enemy populations to allow significant effects of habitat management. Thus, the increase in biocontrol services due to local management is expected to be the greatest in landscapes of an intermediate complexity. Recent studies to test this hypothesis have shown conflicting patterns, with landscape simplicity having positive (e.g. Haenke *et al.*, 2009) or negative (e.g. Winqvist *et al.*, 2011) effects on the benefits of local management practices.

Our goal was to examine the potential interaction between landscape traits and habitat management in a typical field crop agroecosystem of the U.S. Midwest. To do so, we used the soybean aphid and its coccinellid (lady beetle) predators as a model system to elucidate the effects of habitat management and landscape on biocontrol services in soybean fields. Coccinellids are a primary predator of soybean aphid in the north central U.S., with large species like *H. axyridis* and *C. septempunctata* having the highest per capita consumption and accounting for the majority of soybean aphid predation (Costamagna and Landis, 2007). Coccinellid abundance has been correlated with landscape features such as diversity and proportion of non-crop habitat (Gardiner *et al.* 2009) and may respond to floral resources (Harmon *et al.*, 2000). Many coccinellids are known to feed on pollen of a variety of flowering

plant species, including some aphidophagous species commonly found in soybean fields in north central U.S., like *C. septempunctata*, *P. quatuordecimpunctata*, and *C. maculata* (Hodek and Honek 1996). Pollen is an important protein source for carnivorous coccinellids when insect prey are scarce (Hodek and Honek, 1996). Buckwheat is a commonly used flowering resource in habitat management studies because of its demonstrated attractiveness to natural enemies (Fiedler *et al.*, 2008). Additionally, buckwheat strips can serve as a source of alternative prey, like non-pest aphids and the eggs and larvae of lepidopterans and herbivorous beetles.

In this study, we hypothesized that: 1) coccinellid abundance will increase in response to habitat management; 2) predators will significantly suppress soybean aphid populations; 3) biocontrol services will be positively related to habitat diversity within landscapes; and 4) the degree to which habitat management improves biocontrol services will depend on characteristics of the surrounding landscape. To test these hypotheses, we manipulated floral resources adjacent to soybean fields situated in landscapes of varying complexity and composition and measured resultant changes in levels of biocontrol services.

Methods

Site design. This study was replicated in 17 sites across a gradient of landscape diversity in southern Michigan (Figure 1.1; Tables 1.1, 1.2) during the summers of 2008 and 2009. Within a year, each site consisted of two soybean fields, located from 0.5 – 1.8 km apart. In each site, a control field was bordered by a fencerow or grassy field margin, and a treatment field was adjacent to a floral resource strip of annual buckwheat (*Fagopyrum esculentum* cv. Mancan). Hereafter, the control field margin and the buckwheat strip will collectively be referred to as field edges. Within each field, sampling was replicated in four 30 m x 20 m plots (Figure 1.2). In 2008, plots in control fields were set up at least 40 m away from all edges and any non-soybean

vegetation. In the buckwheat fields in 2008 and in both fields in 2009, the plots were set up 15 m away from the buckwheat strip or field margin and at least 40 m away from any non-soybean vegetation on all other sides.

Buckwheat establishment and control margin characteristics. Buckwheat strips were 5 m wide x 200 m in length (Figure 1.2). The strips were planted using a 19 cm row spacing at a rate of 70kg/ha using a Great Plains Seed Drill (Salina, Kansas) along field edges chosen by land owners. In each year, the majority of strips (12 in 2008, 11 in 2009) were planted along fencerows, with the remaining strips planted along woodlots (2 in 2008), driveways or roads (2 in 2008, 5 in 2009), or directly between two crop fields (1 in each year). Strips were planted between 19 May and 6 June in 2008, and between 3 June and 7 July in 2009 (Tables 1.3, 1.4). The strips were planted later in 2009 due to heavy rains in May. After reaching full bloom, buckwheat height and density were measured at 10 random locations within each strip.

Control field margins were chosen to match the cardinal direction of the paired buckwheat strip at each site, except in a few cases where field dimensions made this infeasible. Control field margins were similar to the edges next to which buckwheat strips had been planted (10 at fencerows, 1 next to a woodlot, 3 next to driveways or roads, 1 between crop fields and 2 next to larger patches of mown grass). Vegetation of control field margins consisted of grasses and weedy herbs generally between half a meter and a meter in height.

Aphid counts. Soybean aphid abundance was estimated at weekly intervals using destructive whole plant counts. Five randomly selected soybean plants in each plot were removed and the number of alate and apterous aphids counted. Vegetative and reproductive growth stages for each plant were recorded (Higley and Boethel, 1994).

Coccinellid counts. Aerially dispersing coccinellids were measured in soybean fields and field edges with 23 x 28 cm unbaited yellow sticky cards (PHEROCON AM, Great Lakes IPM, Vestaburg, MI). All coccinellids on the cards were counted and identified to species in the field. Coccinellid voucher specimens were deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University (Table 1.5). In 2008, traps were placed in the center of each plot in all study sites and at two locations within each buckwheat strip. Traps were suspended at 120 cm height from plastic step-in fence posts (Zareba Systems, Lititz, PA) and replaced every week from 1 June to 15 Aug. In 2009, four traps were placed in each field, one in the center of each plot, and three sticky traps were placed in the field edge of both treatment and control fields. The traps in the center of each plot were located 25 m away from the field edge, and were suspended from step-in plastic fence posts at plant canopy height and were replaced every week from 8 June to 26 Aug.

Biocontrol study. The effect of biocontrol services on soybean aphid populations was determined by contrasting soybean aphid population growth in the presence and absence of generalist predators, using methods modified from Gardiner *et al.* (2009). Predators were excluded using cages erected from 7 July to 19 July in 2008 (Table 1.6) and from 9 July to 12 Aug in 2009 (Table 1.7). In each plot a single soybean plant was enclosed in either a 0.84 m tall, 0.30 m diameter (2008) or a 1.07 m tall, 0.36 m diameter (2009) wire tomato support cage. The cages were covered with fine-mesh white netting (openings of 0.65 x 0.17 mm; Skeeta, Bradenton, FL) sewn into sleeves of 137 cm circumference. The bottom of the mesh sleeve was buried in the soil, and the top was tied to a metal “T” post. Each caged plant was paired with an uncaged plant of the same vegetative and reproductive growth stage, located 1 m away in the same row.

Each caged and uncaged plant was infested with 5 aphids in 2008 and 10 aphids in 2009. In both years the aphids were of mixed age classes representing natural colonies in the field. The aphids were transferred using a fine paintbrush from soybean plants in predator exclusion cages established in the soybean fields earlier in the season to rear aphids. Fields in each site were infested with aphids reared in that particular site, except where a field contained insufficient populations. The number of aphids on each caged and uncaged plant was counted at 7 d and 14 d after infestation using non-destructive sampling in the field. Apterous and alate aphids were counted separately, and cages containing more than 10 alates were excluded from analyses to limit the influence of alates that would have normally dispersed to other plants remaining and reproducing within the cages.

Biocontrol services were measured as an index describing the difference in aphid population size with and without naturally occurring predators as a proportion of the exclusion treatment in each site (Gardiner *et al.*, 2009). The Biocontrol Services Index (BSI) was calculated as the difference between the number of aphids on the open plant and on the caged plant, divided by the number of aphids on the caged plant, all at fourteen days after initial infestation.

$$BSI = (Ac - Ao) / Ac$$

Ac = number of aphids on caged plant at 14 d

Ao = number of aphids on open plant at 14 d

BSI values range from 0-1, with 1 representing total aphid suppression and 0 representing no aphid suppression. Negative BSI values created in cases where $Ao > Ac$ were reset to 0. Values of BSI were calculated for each plot in each year, and a field average was calculated.

All cage study results in 2008 are based on 11 sites. Three sites were excluded from the cage study due to the unsuccessful establishment of their buckwheat strips. Three additional sites were excluded from the analysis of cage data due to an inability to successfully establish rearing and experimental cages at the site. All cage study results in 2009 are based on 12 sites. Two sites were not included in the cage study due to the very late blooming of the buckwheat strips in those sites. Two sites were excluded from the analysis because large numbers of alate aphids in the fields during the week of the cage study increased the numbers on the open plants. Two additional sites were excluded due to difficulties in establishing aphid populations due to competing pest populations.

Landscape analysis. Landscapes were assessed by considering all landcover types surrounding each field using the methods of Gardiner (2009). GPS coordinates were collected from the center of each field using a handheld GPS receiver. The GPS coordinates were used to obtain ortho-rectified digital aerial photos for each field from the Michigan Spatial Data Library. Habitats around each field were digitized to a 2.0 km radius using ARC GIS 9.2 (2008) or 9.3 (2009; ESRI Redlands, CA). This range represents a reasonable foraging area of large species of adult ladybeetles. Flights of approximately 1.8 – 2.0 km or greater are considered migratory (i.e. entering or leaving overwintering habitat) for *Hippodamia convergens* (Hodek *et al.*, 1993), a lady beetle species of similar size and diet preferences as the dominant coccinellid predators of soybean aphid. Shorter distances can be considered within the realm of “trivial flights,” or short-distance flights for foraging, which is the type of dispersal relevant for biocontrol in crop fields. Habitat types within field sites were ground-verified each summer and landscape changes were corrected during digitization. During ground-truthing, the specific land cover within all habitat polygons in each landscape was determined by assigning landscape categories to each polygon.

Landscape categories included field crops (primarily corn, soy, wheat, and forage crops) and non-crop habitat types (primarily woodlots, old field, and residential areas) (Table 1.8).

Categories were added for any additional land cover types discovered during ground-truthing. Total area of each habitat category for each site was calculated in ARC GIS 9.2 or 9.3 at four scales: 0.5, 1.0, 1.5, and 2.0 km from the center of the focal field.

Proportion of semi-natural habitat and Simpson's Diversity Index (D) (Simpson, 1949) were used independently as metrics of landscape heterogeneity. Semi-natural habitat included wooded habitats such as forests, woodlots, and fencerows, as well as grassy habitats such as old field and Conservation Reserve Program lands. Simpson's index -- typically used as a measure of species diversity -- is used here as a measure of habitat diversity within each landscape, according to the methods of Gardiner *et al.* (2009).

$$D = \sum p_i^2,$$

where p_i = proportion of landscape occupied by patch type i . Simpson's index is less sensitive than other diversity measures to category richness, in this case habitat richness (Magurran, 2004). Therefore, Simpson's index effectively describes the variance in relative abundance of habitat types without being skewed by the presence of rare habitats (Magurran, 2004).

Diversity decreases as D increases, therefore we calculated $-\ln D$ so that values intuitively increase with increasing diversity. The negative logarithm is preferable to other transformations such as the reciprocal of D , which can create variance problems (Magurran, 2004).

Because seminatural habitat and metrics of habitat diversity have been found to be highly correlated in other studies (e.g. Thies and Tschardtke, 1999; Steffan-Dewenter *et al.*, 2002; Roschewitz *et al.*, 2005b), we calculated Pearson correlation coefficients (PROC CORR, SAS

9.2) for the two landscape variables percentage of seminatural habitat and $-\ln D$ at each landscape extent to determine the degree to which these two metrics measured different components of landscape structure.

Statistical analysis. *Coccinellid abundance:* To test the hypothesis that coccinellid abundance increases in response to habitat management, total coccinellid captures were compared between treatment and control fields, and between buckwheat strips and control field margins. Additionally, the response of coccinellid populations to landscape composition and the interaction between landscape and habitat management were determined. Weekly coccinellid counts were averaged for each field or field margin and analyzed separately for each year using analyses of variance (ANOVA) (PROC GLIMMIX, SAS 9.2). For each response variable (coccinellid abundance in soybean fields in 2008, coccinellid abundance in soybean fields in 2009, and coccinellid abundance in field edges in 2009), eight separate models were run considering either the effect of landscape diversity ($-\ln D$) or proportion of semi-natural habitat measured at 0.5, 1.0, 1.5, or 2.0 km. Fixed effects were treatment, landscape (either $-\ln D$ or semi-natural habitat), and the treatment by landscape interaction. Coccinellid abundance in field edges was log transformed prior to analysis to meet the assumptions of ANOVA. It was unnecessary to transform coccinellid abundance in soybean fields.

Additionally, individual coccinellid species abundance was compared between buckwheat strips and control field margins, as well as between the soybean fields adjacent to buckwheat fields and those without strips. Because of difficulty in meeting distributional assumptions with the data for any individual coccinellid species, nonparametric tests were used. Average summer abundance in each field or field edge were first ranked (PROC RANK, SAS 9.2), such that the field or edge with the highest abundance was given the highest rank. Then,

ranks were compared using mixed model ANOVA (PROC GLIMMIX, SAS 9.2), with treatment as a fixed effect and site as a random effect. ANOVA on rank-transformed data does not depend on the distribution of the data, is resistant to outliers, and is robust to non-normality of errors. However, assumptions regarding homoscedasticity of variance still hold, thus we were only able to compare the relatively common species *H. axyridis*, *C. septempunctata*, *P. quatuordecimpunctata*, *H. variegata*, and *C. maculata* using this method.

Biocontrol study: To test the hypothesis that the presence of predators significantly depresses soybean aphid populations, numbers of aphids on caged and uncaged soybeans were compared. Aphid counts were $\log(x+1)$ transformed prior to analysis to meet the assumptions of homogeneity of variance, and were analyzed using a repeated measures mixed model ANOVA (PROC GLIMMIX, SAS 9.1). Fixed effects were treatment, cage status (i.e., plant caged or uncaged), week and their two- and three-way interactions. Random effects were site and all interaction terms involving site.

Results

Buckwheat establishment. In 2008, buckwheat strips were successfully established in 14 out of 17 sites (Figure 1.3). Three sites were not included in the analysis because of low germination due to flooding or loss to hail. The average height of buckwheat in the 14 strips used in the 2008 study was 89 cm, ranging from 50 cm to 109 cm (Table 1.3). The average density of buckwheat in the 14 strips was $12.2 \text{ stems}/100\text{cm}^2$, ranging from 7.2 to $20.5 \text{ stems}/100\text{cm}^2$. In 2009, 17 strips were successfully established. The average height of all buckwheat strips in 2009 was 57.4 cm, ranging from 20.5 to 93.1 cm (Table 1.4). The average density of all buckwheat strips in 2009 was $7.4 \text{ stems}/100\text{cm}^2$, ranging from 1.4 to $16.8 \text{ stems}/100\text{cm}^2$. Final buckwheat height did not change significantly with planting date in either year (2008: $F_{1,126}=1.85$, $p=0.176$;

2009: $F_{1,153}=0.09$, $p=0.762$), nor did density (2008: $F_{1,126}=0.26$, $p=0.613$; 2009: $F_{1,153}=0.28$, $p=0.600$).

Landscape analysis. The studied landscapes represented a gradient of landscape diversity, with landscapes ranging from forest-dominated to agriculturally-dominated in both years. All landscapes were predominantly made up of corn, soy, wheat, forest, grassland, and residential areas, but proportions of each of these varied between landscapes (Table 1.9, 1.10). In 2008, diversity values ($-\ln D$) ranged from 1.19 to 1.91, while the percentage of semi-natural habitat ranged from 3 to 79% at the 2.0 km scale. In 2009, diversity values ranged from 0.83 to 1.95, with the percentage of semi-natural habitat ranging from 5 to 76 % at the 2.0 km scale. Values were similar for smaller scales.

In 2008, the landscape variables $-\ln D$ and the proportion of semi-natural habitat were not correlated at any scale ($r^2 = -0.11$, $p=0.59$; $r^2 = -0.05$, $p=0.81$; $r^2 = 0.08$, $p=0.69$; $r^2 = 0.05$, $p=0.80$; in descending order of landscape extent). In 2009, these landscape variables were correlated at 2.0, 1.5, and 0.5 km. However, the correlations are low ($r^2 = -0.44$, $p=0.009$; $r^2 = -0.33$, $p=0.05$; $r^2 = 0.34$, $p=0.05$ respectively) and they explain little variation in the two variables. Furthermore, the changing sign of the correlations and the lack of correlation at 1.0 km ($r^2 = -0.24$, $p=0.18$), suggest that these two variables are not closely related within this set of landscapes.

Aphid counts. Soybean aphids naturally colonized all fields used in the study, but populations generally remained below the economic threshold of 250 aphids/ plant (Ragsdale *et al.*, 2007). In 2008, aphids were first detected on 2 June and aphids were discovered in all fields by 17 July (Table 1.6). In 2009, aphids were initially detected during the first week of sampling

(9-12 June) in 6 fields, and all fields were infested by 23 July (Table 1.7). Only one field reached the economic threshold during the last week of sampling in 2009.

Coccinellid abundance. In 2008, 1412 coccinellids were collected and identified in soybean fields. Of these, 90% were exotic species, with 47 % *H. axyridis*, 31% *C. septempunctata*, 10% *P. quatuordecimpunctata*, and 2% *H. variegata*. The most common native species were *C. maculata* and *H. parenthesis*, which made up 6% and 2% of the total capture, respectively. All other species made up 1% or less of captures. In 2009, 4276 coccinellids were collected and identified in soybean fields. The majority were exotic species, with 33% *C. septempunctata*, 28% *H. axyridis*, 18% *P. quatuordecimpunctata*, and 9% *H. variegata*. The most common native species were *C. maculata* and *H. parenthesis*, which made up 5% and 3% of the total capture, respectively. All other species made up 1% or less of captures.

Habitat manipulation altered predator abundance, with significantly more coccinellids found in buckwheat strips than in control field edges in 2009, the only year for which the comparison was made (Table 1.11, Figure 1.4). An average of 2.69 ± 0.42 lady beetles per card were found in the buckwheat strips, as compared to an average of 1.32 ± 0.21 per card in the control field margins.

Slightly more coccinellids were captured in fields with buckwheat strips than in control fields in both years, although the effect was not significant in either year (Table 1.12; Figure 1.4). Coccinellid abundance in fields was not affected by landscape diversity at any scale in either year, nor by the diversity by treatment interaction (Table 1.11). However, in 2009, lady beetles were more abundant in soybean fields surrounded by landscapes with greater proportions of semi-natural habitat measured at 1.5 and 2.0 km (Table 1.11, Figure 1.4). The treatment by landscape interaction for this effect was not significant at any scale. . Statistical results for all

effects were identical at the 1.5 and 2.0 km scales, while no effect of landscape was shown at smaller scales.

Within buckwheat strips, 81 % of lady beetles captured were exotic species (*C. septempunctata* 28%, *H. variegata* 25%, *P. quatordecimpunctata* 20%, *H. axyridis* 8%). The native pink lady beetle *C. maculata* made up an additional 9% and the orange spotted lady beetles *Brachiacanthus* sp. made up an additional 4% of the lady beetles found in buckwheat strips. In contrast, there were more *H. axyridis* (17%) and fewer *H. variegata* (3%) in the control field margins. Proportions of other lady beetles were similar (*C. septempunctata* 24%, *P. quatordecimpunctata* 34%, *C. maculata* 4%, *Brachiacanthus* sp. 8%). However, the abundance of lady beetles in field margins did not vary with landscape diversity or amount of semi-natural habitat in the landscape in either year (Table 1.11).

While rank comparisons showed no difference in species abundance between treatment and control fields in 2008 (Table 1.12), several coccinellid species were significantly more abundant in buckwheat strips than in control field edges in 2009 (Table 1.13). Using rank abundance, three common exotic species *C. septempunctata*, *H. variegata*, and *P. quatordecimpunctata*, as well as the common native species *C. maculata*, were more commonly found in buckwheat strips. *C. maculata* was also found to be more abundant in fields next to buckwheat strips than in fields next to control field margins. In contrast, no species was found to be more abundant in control field margins, and only *H. axyridis* was more common in control soybean fields.

Biocontrol study. Exclusion of natural enemies resulted in dramatically increased soybean aphid populations in both years (Figure 1.5). Across fields and sites, the number of aphids on caged plants from which predators were excluded was significantly higher than on

uncaged plants which were exposed to predators (2008: $F_{1,10}=251.33$, $p<0.0001$; 2009: $F_{1,10}=114.03$, $p<0.0001$). After 14 days, there were 38 fold more aphids per plant on caged than uncaged plants in 2008, and 53 fold more aphids per plant on caged than uncaged plants 2009. Buckwheat treatment did not significantly affect the size of the difference in aphid populations on caged and uncaged plants in either year (2008: $F_{1,10}=1.62$, $p=0.2313$; 2009: $F_{1,10}=0.62$, $p=0.4509$), nor were any of the interactions involving treatment significant in either year. The differences in aphid populations between caged and uncaged plants were greater at 14 days than at 7 days in both years (Figure 1.5), as indicated by a significant week by cage status interaction (2008: $F_{1,10}=61.06$, $p<0.0001$; 2009: $F_{1,10}=30.03$, $p=0.0003$).

We found very high suppression of aphids by the existing predator populations in both years in almost all fields. BSI values in 2008 ranged from 0.77 to 1, with an average value of 0.954 ± 0.01 and 22 of 23 fields had BSI values greater than 0.90 (Table 1.14). BSI values in 2009 ranged from 0.66 to 0.99, with an average value of 0.954 ± 0.02 and 20 of 23 fields had BSI values of greater than 0.90 (Table 1.14). We did not conduct landscape analyses on BSI because of a lack of variation available to be explained by this or any other variable.

Discussion

Landscape effects on local management to improve services. In this study, predators had a significant negative impact on soybean aphid populations and lady beetle abundance increased both in habitat management strips and with the proportion of semi-natural habitat in the landscape, but we found no interaction between landscape context and local habitat management on coccinellid abundance. In contrast, other studies have found that the degree to which local management can influence communities is dependent upon the degree of

heterogeneity in the surrounding landscape. Local management was more effective for increasing richness and abundance in simplified, crop-dominated landscapes than in diverse landscapes for a variety of taxa (e.g. pollinators, (Carvell *et al.*, 2011); bees, (Holzschuh *et al.*, 2007; Rundlof *et al.*, 2008); butterflies, (Rundlof and Smith, 2006); birds, (Geiger *et al.*, 2010; Smith *et al.*, 2010); aphidophagous syrphids, (Haenke *et al.*, 2009); and plants, (Roschewitz *et al.*, 2005a)). In contrast, Winqvist *et al.* (2011) demonstrated the opposite effect, with organic farming methods increasing biocontrol over conventional methods only in the most diverse landscapes.

Additionally, other studies have shown little impact of local management at all, with taxon diversity and abundance responding primarily to landscape composition alone (Purtauf *et al.*, 2005; Schmidt *et al.*, 2005). These contrasting results may indicate that these relationships are highly taxon- and context-dependent. Indeed, even within a single study, different taxa exhibited opposite responses to landscape and local management (Concepcion *et al.*, 2008), while a recent meta-analysis showed that the arthropod response to local management was influenced by landscape context for populations in cropland habitats but not within grassland habitats (Batáry *et al.*, 2011).

Effects of local management on coccinellid beetles. The habitat management treatment successfully attracted coccinellid beetles, with significantly more lady beetles in buckwheat strips than in grassy field margins or fencerows. However, this increase in coccinellid abundance at the field edges was not reflected in higher abundance in adjacent soybean fields. Other studies have similarly demonstrated predators taking advantage of managed habitats without clear effects on adjacent fields. For example, a guinea grass border did not affect the abundance of predators within maize or the density of spotted stem borer, *Chilo partellus*, in spite of attracting abundant predators to the strip (Koji *et al.*, 2007). In contrast, Walton and Isaacs (2011) found

significantly higher abundance of both syrphid flies and predatory wasps in blueberry fields adjacent to native wildflower plantings than next to mown grass strips. In other cases, increased natural enemy abundance from floral resource strips have resulted in higher parasitism rates (Langer and Hance, 2004) and lower pest abundance in adjacent fields (Hickman and Wratten, 1996). Inconsistencies in these patterns could be a result of varying predator biology or landscape context.

Landscape effects on coccinellid beetles. In 2009, abundance of coccinellids in soybean fields increased with proportion of semi-natural habitat in the surrounding landscape. Similar positive effects of semi-natural habitat on natural enemies have been found for a variety of predatory and parasitic taxa (Chaplin-Kramer *et al.*, 2011). Lady beetles require undisturbed habitat for overwintering, and *H. axyridis*, one of the two most abundant species collected in our study, is known to overwinter in wooded areas. The abundance of potential overwintering sites in landscapes with large proportions of semi-natural habitat could have led to higher overwinter survival of coccinellids in those landscapes, leading to larger populations emerging in the spring. Additionally, lady beetles in the north central U.S. emerge from overwintering in March and April, before field crops such as corn and soy are planted in May or June. Thus, lady beetles are dependent upon other food sources in the spring before foraging on soybean aphid in the summer. Aphids in semi-natural habitat, such as those feeding on grasses or legumes in old fields, could provide an abundant food source in the spring, allowing lady beetles in these landscapes to build up larger populations by the time field crops are planted in summer.

In other studies, seminatural habitat has been used as a metric of landscape heterogeneity, as in European landscapes it has been repeatedly found to be highly correlated with Shannon habitat diversity (e.g. Thies and Tscharntke, 1999; Steffan-Dewenter *et al.*, 2002; Roschewitz *et al.*,

2005b). In our study, however, Simpson's Diversity, a similar metric, was not strongly correlated with seminatural habitat at any scale. This could be because European landscapes are functionally different than landscapes in the north central U.S. Alternatively, the landscapes examined in this study may represent a greater maximum amount of seminatural habitat. In the European studies cited, maximum semi-natural habitat was usually around 30 – 50%, whereas in this study semi-natural habitat was as high as 79%. It is possible that the relationship between habitat diversity and seminatural habitat breaks down at high levels of seminatural habitat because of dominance of one or two habitat types. A landscape may have a large proportion of seminatural habitat and low diversity if, for example, it is dominated by a single seminatural landcover type such as forest. In our study, semi-natural habitat was a better predictor of coccinellid abundance than habitat diversity. This may be because a single type of seminatural habitat can still provide multiple resources, such as nesting and overwintering habitats, temporary refuges, alternative prey and floral resources (Bianchi *et al.*, 2006).

In contrast to the effect on lady beetles in crop fields, there was no effect of semi-natural habitat on coccinellid abundance within the buckwheat strips. Haenke *et al.* (2009) found that the abundance and species richness of syrphid flies in flower strips was positively related to the amount of cropland in the surrounding landscape, presumably because the addition of floral resources was more rewarding in crop-dominated landscapes than in diverse landscapes with abundant resources. This suggests that coccinellids used the flowering buckwheat strips regardless of the availability of other resources in the surrounding landscapes.

Effects of predators on soybean aphid density. Predators provided high levels of biological control of soybean aphid in all sites. Regardless of landscape conditions or habitat management, soybean aphid populations exposed to ambient predator densities were greatly

suppressed compared to the predator exclusion treatment. In light of the fact that the abundance of the major predators of soybean aphid in this system, coccinellid beetles, was positively related to the proportion of semi-natural habitat in the landscape surrounding study fields, it is somewhat surprising that biocontrol services were not similarly lower in crop dominated landscapes and higher in landscapes with more semi-natural habitats. The high levels of biocontrol in all landscapes suggests that even the lowest abundance of coccinellids was sufficient to control soybean aphid. This result stands in stark contrast to those of Gardiner *et al.* (2009) who found that both coccinellid abundance and soybean aphid suppression were correlated with habitat diversity and abundance of non-crop habitat in surrounding landscapes. This may indicate a shift in this system from 2005-06 when Gardiner and others (2009) collected their data to 2008-09 when the data for this paper were collected. Elton (1958) postulated that changes within biological communities that lead to increased competition and predation or parasitism of exotics may be responsible for the transition of some exotic species from highly invasive to merely naturalized members of the community. In a similar fashion, the predominant predators of the soybean aphid, *H. axyridis* and *C. septempunctata*, may have become a greater proportion of the existing natural enemy community in response to the abundant food source provided by soybean aphids (Heimpel *et al.*, 2010), thereby helping to suppress further aphid outbreaks. As further evidence, soybean aphid and *H. axyridis* populations were initially cyclic, with aphid outbreak years (2001, 2003, and 2005), followed by high populations of *H. axyridis* in 2002, 2004, and 2006 (Knapp *et al.* 2012). However, no soybean aphid outbreaks have occurred in Michigan since 2005 and aphids and *H. axyridis* have not cycled since then, possibly indicating that a new equilibrium has been reached in this system. Alternatively, management changes within soybean fields could have limited the ability of soybean aphid populations to increase unchecked

throughout the growing season. Modeling studies indicate that in order to prevent soybean aphid outbreaks, it is important for natural enemies to consume insipient aphid colonies before they become well established and produce alates (Costamagna and Landis, 2011). In the past, initial soybean aphid colonization of Midwestern soy fields occurred early in the season when coccinellids have had limited time to increase from their overwintering populations. Increased use of soybean seed treated with systemic insecticide in recent years (Magalhaes *et al.*, 2008) may delay aphid population growth in soybean fields, giving natural enemy populations time to increase on alternative hosts and prey before soybean aphids become well-established.

Conclusions

In this study, landscape characteristics and local habitat affected soybean aphid natural enemies in different ways. At a local scale, coccinellid abundance increased within the managed habitats. Thus, within the same landscapes they were more commonly captured in flowering buckwheat strips than in typical field edge habitat such as grassy margins or fencerows. In contrast, overall coccinellid population levels in equivalent habitats (i.e. paired soybean fields) were influenced by the abundance of semi-natural habitat at the landscape scale. This makes sense in light of the large distances over which coccinellid species such as *H. axyridis* and *C. septempunctata* disperse and forage. Furthermore, we found no evidence of an interaction between local management and landscape diversity or semi-natural habitat in this study. Coccinellid response in soybean fields to landscape-scale semi-natural habitat was not affected by the presence of adjacent buckwheat strips, indicating that for this pest, landscape characteristics override the effect of enhanced local resources. This suggests that to manage for increased biocontrol services of soybean aphid will require a focus on manipulating overall landscape structure rather than local resources.

However, as the studies reviewed above suggest, the influences of landscape characteristics on the relationship between local habitats and natural enemy populations are likely system-specific and dependent upon the biology of the natural enemies in question. Soybean aphid is not the only pest of soybean in these landscapes and other crops have additional pest-natural enemy associations that may be successfully managed at local scales. A greater understanding of these complex relationships will enable growers and researchers to develop more effective management systems suited to specific landscapes, prevailing pests, and their natural enemy communities. Thus, we may anticipate that in the future a combination of local and landscape management practices may be required to maximize overall pest suppression in the larger agroecosystem.

APPENDIX

Chapter I Tables and Figures

Table 1.1: Township, county and coordinates from soybean treatment and control fields used in 2008.

Site	County	Treatment field		Control field	
		Longitude	Latitude	Longitude	Latitude
Cassopolis	Cass	85° 58' 26.97"W	41° 59' 58.15"N	85° 59' 5.05"W	41° 59' 49.89"N
Leroy	Calhoun	85° 12' 57.38"W	42° 10' 2.46"N	85° 11' 55.4"W	42° 9' 54.72"N
Vicksburg	Kalamazoo	85° 31' 54.45"W	42° 6' 46.86"N	85° 31' 12.52"W	42° 6' 16.43"N
Springport	Jackson	84° 38' 30.91"W	42° 25' 5.02"N	84° 37' 48.15"W	42° 25' 15.87"N
Stockbridge	Ingham	84° 11' 57.12"W	42° 32' 21.76"N	84° 12' 3.01"W	42° 31' 46.35"N
Mason	Ingham	84° 25' 46.29"W	42° 32' 31.71"N	84° 26' 4.51"W	42° 32' 37.2"N
Fowlerville	Livingston	84° 5' 58.49"W	42° 44' 56.09"N	84° 6' 2.66"W	42° 44' 27.05"N
Westphalia	Clinton	84° 47' 46.38"W	42° 52' 21.92"N	84° 47' 52.92"W	42° 52' 27.37"N
Vermontville	Eaton	84° 58' 45.88"W	42° 38' 29.62"N	84° 57' 55.92"W	42° 38' 31.12"N
Charlotte	Eaton	84° 53' 49.79"W	42° 32' 12.39"N	85° 0' 19.9"W	42° 32' 11.78"N
Ithaca	Gratiot	84° 37' 10.78"W	43° 11' 32.22"N	84° 36' 55.46"W	43° 11' 26.03"N
Breckenridge	Gratiot	84° 30' 11.98"W	43° 21' 13.22"N	84° 31' 2.51"W	43° 20' 55.71"N
Saginaw	Saginaw	84° 6' 55.80"W	43° 22' 50.30"N	84° 6' 44.83"W	43° 22' 28.23"N
Lapeer	Lapeer	83° 18' 50.30"W	42° 58' 54.60"N	83° 18' 11.23"W	42° 58' 57.74"N
Richfield	Genesee	83° 29' 38.31"W	43° 5' 29.61"N	83° 29' 7.29"W	43° 5' 24.35"N
Fostoria	Tuscola	83° 23' 9.50"W	43° 14' 59.16"N	83° 23' 16.99"W	43° 15' 1.01"N
Silverwood	Lapeer	83° 13' 3.61"W	43° 17' 16.77"N	83° 13' 8.32"W	43° 17' 16.34"N

Table 1.2: Township, county and coordinates from soybean treatment and control fields used in 2009.

Site	County	Treatment field		Control field	
		Longitude	Latitude	Longitude	Latitude
Cassopolis	Cass	85° 59' 21.84" W	41° 59' 51.72" N	85° 59' 4.96" W	41° 59' 49.85" N
Leroy	Calhoun	85° 11' 38.15" W	42° 9' 57.91" N	85° 11' 59.34" W	42° 10' 17.43" N
Vicksburg	Kalamazoo	85° 30' 16.07" W	42° 05' 08.15" N	85° 29' 42.06" W	42° 6' 3.15" N
Springport	Jackson	84° 37' 55.12" W	42° 24' 52.63" N	84° 37' 59.70" W	42° 25' 11.78" N
Charlotte	Eaton	85° 1' 14.52" W	42° 29' 39.82" N	85° 1' 14.36" W	42° 29' 16.15" N
Vermontville	Eaton	85° 0' 2.16" W	42° 41' 46.31" N	85° 0' 10.43" W	42° 41' 47.75" N
Westphalia	Clinton	85° 47' 50.40" W	42° 51' 46.02" N	85° 47' 44.23" W	42° 52' 10.13" N
Stockbridge	Ingham	84° 12' 13.94" W	42° 32' 23.25" N	84° 12' 8.12" W	42° 31' 49.22" N
Mason	Ingham	84° 26' 8.93" W	42° 32' 35.13" N	84° 25' 56.34" W	42° 32' 40.31" N
Fowlerville	Livingston	84° 6' 13.69" W	42° 45' 1.93" N	84° 6' 46.02" W	42° 44' 14.14" N
Grand Blanc	Genesee	83° 40' 55.56" W	42° 53' 13.55" N	83° 40' 57.35" W	42° 53' 28.31" N
Oxford 1	Oakland	83° 14' 21.84" W	42° 51' 37.80" N	83° 14' 20.04" W	42° 51' 52.91" N
Oxford 2	Oakland	83° 18' 55.80" W	42° 51' 19.07" N	83° 18' 46.43" W	42° 51' 24.47" N
Metamora	Lapeer	83° 15' 10.80" W	42° 56' 35.16" N	83° 15' 21.23" W	42° 56' 34.79" N
Ithaca	Gratiot	84° 33' 57.23" W	43° 12' 57.23" N	84° 34' 37.19" W	43° 13' 6.59" N
Breckenridge	Gratiot	84° 30' 9.72" W	43° 21' 17.64" N	84° 30' 17.64" W	43° 20' 25.07" N
Silverwood	Lapeer	83° 12' 48.54" W	43° 17' 18.21" N	83° 13' 8.28" W	43° 17' 16.28" N

Table 1.3: Buckwheat strip data for 2008, including date each strip was planted and subsequently reached full bloom. Density (stems/10 cm²) and height (cm) measurements were taken at full bloom.

Site	Planting date	Full bloom	Density	Height
Cassopolis	2 June	30 June	20.5 ± 1.62	95.7 ± 4.57
Leroy	2 June	7 July	19.6 ± 1.58	50.4 ± 8.81
Vicksburg	30 May	7 July	8.3 ± 1.02	69.6 ± 6.09
Springport	30 May	30 June	9.4 ± 0.69	86.4 ± 5.51
Stockbridge	19 May	1 July	16.6 ± 18.7	89.9 ± 6.55
Mason	19 May	1 July	16 ± 1.58	68.4 ± 4.87
Fowlerville	19 May	1 July	7.2 ± 0.51	128.7 ± 7.05
Westphalia	6 June	no record	2 ± 0.71	43.5 ± 13.36
Vermontville	6 June	no record	2 ± 0.76	36.7 ± 10.4
Charlotte	28 May	no record	n/a	n/a
Ithaca	28 May	3 July	8.5 ± 0.96	82.9 ± 4.04
Breckenridge	28 May	3 July	8.9 ± 0.6	108.5 ± 5.58
Saginaw	28 May	3 July	8.1 ± 0.55	87.5 ± 5.21
Lapeer	23 May	26 June	10.4 ± 0.64	74.6 ± 6.1
Richfield	23 May	26 June	9.4 ± 0.52	107.9 ± 6.38
Fostoria	23 May	26 June	14.2 ± 0.99	113.1 ± 4.26
Silverwood	23 May	8 July	13.5 ± 1.0	80.9 ± 6.54

Table 1.4: Buckwheat strip data for 2009, including date each strip was planted and subsequently reached full bloom. Density (stems/10 cm²) and height (cm) measurements were taken at full bloom.

Site	Planting Date	Full Bloom	Density	Height
Cassopolis	16 June	20 July	3.90 ± 0.75	22.10 ± 2.52
Leroy	16 June	20 July	3.60 ± 0.82	45.30 ± 8.37
Vicksburg	16 June	20 July	3.00 ± 1.13	57.20 ± 14.37
Springport	10 June	15 July	4.70 ± 0.52	55.30 ± 6.06
Charlotte	10 June	16 July	6.40 ± 1.07	64.80 ± 4.23
Vermontville	16 June	23 July	5.50 ± 0.81	76.30 ± 6.80
Westphalia	3 June	9 July	16.80 ± 1.28	58.05 ± 5.42
Stockbridge	7 July	5 Aug	11.00 ± 1.15	66.30 ± 6.58
Mason	10 June	22 July	15.90 ± 0.84	67.00 ± 2.27
Fowlerville	7 July	19 Aug	11.50 ± 0.91	89.20 ± 2.74
Grand Blanc	24 June	29 July	7.10 ± 1.03	39.20 ± 2.80
Oxford 1	24 June	10 Aug	6.00 ± 1.12	71.10 ± 3.06
Oxford 2	24 June	28 July	1.40 ± 0.37	20.50 ± 6.03
Metamora	24 June	28 July	4.30 ± 1.58	31.50 ± 6.79
Ithaca	3 June	17 July	6.60 ± 1.10	81.75 ± 3.46
Breckenridge	3 June	6 July	6.50 ± 0.85	93.10 ± 3.24
Silverwood	3 June	14 July	11.30 ± 1.64	37.40 ± 5.37

Table 1.5: Record of deposition of voucher specimens for Chapter I. The specimens listed below have been deposited in the Albert J. Cook Arthropod Research Collection, Michigan State University (MSU) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number 2013-08 have been attached or included in fluid preserved specimens.

Family	Genus-Species	Life Stage	Quantity	Preservation
Coccinellidae	<i>Coccinella septempunctata</i>	Adult	3	Pinned
Coccinellidae	<i>Harmonia axyridis</i>	Adult	3	Pinned
Coccinellidae	<i>Hippodamia variegata</i>	Adult	3	Pinned
Coccinellidae	<i>Propylea quatuordecimpunctata</i>	Adult	3	Pinned
Coccinellidae	<i>Coleomegilla maculata</i>	Adult	3	Pinned
Coccinellidae	<i>Cycloneda munda</i>	Adult	2	Pinned
Coccinellidae	<i>Hippodamia parenthesis</i>	Adult	2	Pinned
Coccinellidae	<i>Hippodamia glacialis</i>	Adult	1	Pinned
Coccinellidae	<i>Hippodamia convergens</i>	Adult	1	Pinned
Coccinellidae	<i>Hippodamia tredecimpunctata</i>	Adult	1	Pinned
Coccinellidae	<i>Brachiacanthus ursina</i>	Adult	2	Pinned
Coccinellidae	<i>Brachiacanthus undulata</i>	Adult	1	Pinned
Coccinellidae	<i>Psyllobora vigintimaculata</i>	Adult	1	Pinned
Aphididae	<i>Aphis glycines</i>	Adults, nymphs		70% EtOH

Table 1.6: Dates soybean aphids were first detected in each treatment and control field, and dates cage study was conducted in each site in 2008.

Site	Aphid detection treatment	Aphid detection control	Cage study
Cassopolis	16 June	30 June	14-28 July
Leroy	7 July	30 June	16-30 July
Vicksburg	16 June	3 June	11-25 July
Springport	3 June	3 June	n/a
Stockbridge	3 June	3 June	18 July-1 Aug
Mason	3 June	16 June	10-24 July
Fowlerville	11 June	10 July	23 July - 6 Aug
Westphalia	4 June	4 June	n/a
Vermontville	4 June	4 June	11-25 July
Charlotte	12 June	6 June	n/a
Ithaca	4 June	4 June	13-27 July
Breckenridge	18 June	18 June	7-21 July
Saginaw	11 June	11 June	8-22 July
Lapeer	10 June	10 June	15-29 July
Richfield	2 June	2 June	9-23 July
Fostoria	9 June	9 June	17-31 July
Silverwood	17 July	8 August	17-31 July

Table 1.7: Dates soybean aphids were first detected in each treatment and control field, and date cage study was conducted in each site in 2009.

Site	Aphid detection treatment	Aphid detection control	Cage study
Cassopolis	30 June	30 June	20 July - 3 Aug
Leroy	16 June	16 June	20 July - 3 Aug
Vicksburg	23 June	6 July	20 July - 3 Aug
Springport	8 July	1 July	15-29 July
Charlotte	30 July	23 July	16-30 July
Vermontville	12 June	24 June	23 July-6 Aug
Westphalia	16 July	22 June	9-23 July
Stockbridge	11 June	11 June	n/a
Mason	1 July	16 June	15-29 July
Fowlerville	11 June	25 June	n/a
Grand Blanc	8 July	29 June	12-26 Aug
Oxford 1	22 June	11 June	28 July -10 Aug
Oxford 2	15 June	22 June	10-24 Aug
Metamora	11 June	14 July	10-24 Aug
Ithaca	17 July	9 June	10-24 July
Breckenridge	24 July	17 July	10-24 July
Silverwood	14 July	7 July	14-28 July

Table 1.8: A) Crop and B) non-crop land covers found in landscapes surrounding study fields. All land covers found were used to calculated Simpson's diversity metric ($-\ln D$). The categories of grassland and forest land covers were subsequently combined into "semi-natural habitat" for landscape analyses.

A) Crop land covers	B) Non-crop land covers
<i>Major annual crops</i>	<i>Grasslands</i>
Soy	Remnant prairie
Corn	Old Field
Wheat	CRP lands
<i>Forage crops</i>	<i>Forest</i>
Alfalfa	Forest
Pasture	Woodlots
Orchard grass	Hedgerows/ fencerows
<i>Less common annual crops</i>	<i>Residential</i>
Dry beans	Urban
Sugar beats	Residential/ suburban
Fruit	Mowed turf (golf course, cemetery)
Unidentified small grains	<i>Less common non-crop covers</i>
	Unplanted, tilled field
	Gravel quarry
	Open Water
	Wetland

Table 1.9: Simpson's diversity metric and proportion of each major land cover type surrounding study fields at the 2 km scale in 2008.

Site	-lnD	Soy	Corn	Wheat	Forest	Grasslands	Residential	Semi-natural
<i>Landscape surrounding treatment field</i>								
Breckenridge	1.189	0.24	0.47	0.13	0.02	0.02	0.02	0.04
Cassopolis	1.272	0.15	0.45	0.00	0.22	0.13	0.05	0.35
Leroy	1.376	0.07	0.08	0.07	0.46	0.16	0.13	0.62
Lapeer	1.403	0.05	0.02	0.05	0.43	0.30	0.12	0.73
Westphalia	1.536	0.28	0.33	0.08	0.10	0.17	0.05	0.26
Vermontville	1.563	0.25	0.16	0.00	0.31	0.22	0.05	0.53
Fostoria	1.609	0.28	0.10	0.05	0.30	0.13	0.11	0.43
Springport	1.615	0.16	0.24	0.05	0.32	0.13	0.05	0.45
Saginaw	1.623	0.21	0.14	0.04	0.34	0.09	0.09	0.42
Vicksburg	1.695	0.05	0.10	0.02	0.29	0.11	0.32	0.40
Ithaca	1.719	0.20	0.30	0.14	0.12	0.19	0.06	0.31
Stockbridge	1.722	0.22	0.22	0.13	0.23	0.12	0.05	0.35
Charlotte	1.740	0.22	0.19	0.08	0.27	0.15	0.06	0.42
Richfield	1.769	0.22	0.07	0.02	0.26	0.18	0.20	0.44
Fowlerville	1.816	0.16	0.26	0.02	0.21	0.23	0.09	0.44
Silverwood	1.818	0.26	0.13	0.21	0.13	0.21	0.04	0.34
Mason	1.911	0.15	0.18	0.04	0.23	0.19	0.17	0.42

Table 1.9 (cont'd).

Site	-lnD	Soy	Corn	Wheat	Forest	Grasslands	Residential	Semi-natural
<i>Landscape surrounding control field</i>								
Breckenridge	1.142	0.27	0.47	0.08	0.00	0.03	0.02	0.03
Leroy	1.170	0.06	0.09	0.06	0.52	0.08	0.16	0.60
Lapeer	1.210	0.06	0.02	0.01	0.49	0.29	0.11	0.79
Cassopolis	1.308	0.17	0.43	0.00	0.21	0.14	0.05	0.35
Westphalia	1.515	0.27	0.34	0.06	0.09	0.18	0.05	0.27
Vermontville	1.569	0.19	0.10	0.01	0.36	0.25	0.05	0.61
Springport	1.597	0.21	0.23	0.06	0.31	0.08	0.04	0.39
Richfield	1.609	0.16	0.07	0.03	0.36	0.17	0.16	0.54
Ithaca	1.614	0.19	0.36	0.10	0.09	0.17	0.06	0.27
Fostoria	1.673	0.26	0.10	0.06	0.29	0.16	0.11	0.45
Saginaw	1.674	0.21	0.23	0.04	0.26	0.11	0.08	0.37
Charlotte	1.726	0.23	0.18	0.08	0.28	0.14	0.05	0.42
Vicksburg	1.765	0.08	0.18	0.03	0.27	0.10	0.25	0.37
Stockbridge	1.772	0.20	0.25	0.12	0.20	0.15	0.05	0.35
Fowlerville	1.794	0.16	0.28	0.04	0.18	0.25	0.08	0.42
Silverwood	1.889	0.23	0.17	0.18	0.14	0.23	0.04	0.38
Mason	1.889	0.14	0.17	0.04	0.24	0.20	0.20	0.43

Table 1.10: Simpson's diversity metric and proportion of each major land cover type surrounding study fields at the 2 km scale in 2009.

Site	-lnD	Soy	Corn	Wheat	Forest	Grasslands	Residential	Semi-natural
<i>Landscape surrounding treatment fields</i>								
Metamora	0.828	0.04	0.01	0.00	0.65	0.11	0.08	0.76
Cassopolis	1.196	0.14	0.47	0.02	0.24	0.07	0.05	0.32
Leroy	1.240	0.16	0.02	0.03	0.49	0.10	0.15	0.59
Breckenridge	1.311	0.38	0.28	0.07	0.01	0.04	0.02	0.05
Grand Blanc	1.391	0.05	0.07	0.00	0.38	0.17	0.27	0.56
Vermontville	1.481	0.22	0.33	0.01	0.25	0.09	0.06	0.34
Silverwood	1.499	0.40	0.17	0.06	0.14	0.13	0.04	0.27
Vicksburg	1.574	0.21	0.26	0.03	0.29	0.05	0.05	0.35
Charlotte	1.575	0.20	0.13	0.08	0.36	0.16	0.04	0.52
Stockbridge	1.610	0.22	0.28	0.18	0.18	0.06	0.05	0.24
Oxford Liptons	1.675	0.05	0.02	0.01	0.35	0.21	0.20	0.56
Ithaca	1.725	0.22	0.30	0.12	0.12	0.10	0.10	0.22
Springport	1.753	0.14	0.19	0.06	0.30	0.05	0.05	0.35
Westphalia	1.765	0.19	0.29	0.09	0.17	0.17	0.05	0.34
Oxford	1.783	0.21	0.02	0.00	0.30	0.29	0.09	0.59
Mason	1.920	0.15	0.16	0.06	0.25	0.13	0.24	0.38
Fowlerville	1.951	0.19	0.13	0.05	0.24	0.24	0.10	0.49

Table 1.10 (cont'd).

Site	-lnD	Soy	Corn	Wheat	Forest	Grasslands	Residential	Semi-natural
<i>Landscape surrounding control fields</i>								
Metamora	0.835	0.06	0.00	0.00	0.65	0.11	0.08	0.76
Cassopolis	1.204	0.13	0.48	0.02	0.22	0.10	0.05	0.32
Grand Blanc	1.292	0.05	0.05	0.00	0.40	0.18	0.29	0.58
Leroy	1.377	0.18	0.03	0.03	0.43	0.13	0.15	0.57
Breckenridge	1.396	0.31	0.35	0.13	0.02	0.05	0.02	0.07
Vermontville	1.486	0.24	0.31	0.01	0.26	0.09	0.06	0.34
Silverwood	1.524	0.40	0.15	0.05	0.15	0.13	0.04	0.28
Vicksburg	1.532	0.27	0.22	0.00	0.30	0.06	0.08	0.36
Westphalia	1.647	0.21	0.34	0.10	0.11	0.16	0.06	0.28
Charlotte	1.655	0.19	0.12	0.12	0.34	0.15	0.04	0.49
Oxford Liptons	1.661	0.05	0.02	0.01	0.35	0.17	0.19	0.53
Oxford	1.668	0.20	0.02	0.00	0.34	0.24	0.10	0.59
Springport	1.707	0.17	0.20	0.05	0.31	0.05	0.05	0.36
Stockbridge	1.711	0.20	0.27	0.16	0.19	0.11	0.05	0.30
Ithaca	1.802	0.24	0.24	0.13	0.14	0.13	0.10	0.26
Fowlerville	1.855	0.15	0.21	0.06	0.26	0.22	0.08	0.48
Mason	1.923	0.15	0.14	0.07	0.26	0.13	0.22	0.38

Table 1.11: Effects of landscape and local habitat management on coccinellid abundance in 2008 soybean fields, 2009 soybean fields, and 2009 field margins. Separate analyses were run with A) Simpson's diversity index $-\ln D$, and with B) proportion of semi-natural habitat in the landscape as the landscape descriptor variables. Results are shown for landscape values at the 2.0 km scale, but were consistent at all scales

A			B		
2008 Soy Fields					
	F value	pr > F		F value	pr > F
Buckwheat treatment	$F_{1,24}=2.72$	0.112	Buckwheat treatment	$F_{1,24}=0.59$	0.451
Diversity ($-\ln D$)	$F_{1,24}=1.15$	0.295	semi-natural habitat	$F_{1,24}=0.07$	0.798
treatment* $-\ln D$	$F_{1,24}=2.18$	0.153	treatment*semi-natural	$F_{1,24}=1.81$	0.191
2009 Soy Fields					
	F value	pr > F		F value	pr > F
Buckwheat treatment	$F_{1,30}=0.19$	0.662	Buckwheat treatment	$F_{1,30}=0.47$	0.496
Diversity ($-\ln D$)	$F_{1,30}=0.14$	0.713	semi-natural habitat	$F_{1,30}=6.11$	0.019
treatment* $-\ln D$	$F_{1,30}=0.31$	0.580	treatment*semi-natural	$F_{1,30}=0.19$	0.667
2009 Field Margins					
	F value	pr > F		F value	pr > F
Buckwheat treatment	$F_{1,30}=10.58$	0.003	Buckwheat treatment	$F_{1,30}=10.78$	0.003
Diversity ($-\ln D$)	$F_{1,30}=0.00$	0.889	semi-natural habitat	$F_{1,30}=0.25$	0.618
treatment* $-\ln D$	$F_{1,30}=0.03$	0.834	treatment*semi-natural	$F_{1,30}=0.40$	0.532

Table 1.12: Mean $\pm$ S.E. of coccinellid beetles of each species found in soybean fields or field margins during 2008. No comparisons between treatment and control fields were significant in this year.

Coccinellids	Buckwheat strip	Treatment field	Control field
EXOTIC SPECIES			
<i>Harmonia axyridis</i>	0.32 $\pm$ 0.04	0.64 $\pm$ 0.05	0.52 $\pm$ 0.04
<i>Coccinella septempunctata</i>	0.87 $\pm$ 0.10	0.41 $\pm$ 0.03	0.35 $\pm$ 0.03
<i>Hippodamia variegata</i>	0.007 $\pm$ 0.005	0.02 $\pm$ 0.01	0.02 $\pm$ 0.01
<i>Propylea quatuordecimpunctata</i>	0.24 $\pm$ 0.03	0.15 $\pm$ 0.02	0.10 $\pm$ 0.01
NATIVE SPECIES			
<i>Coleomegilla maculata</i>	0.11 $\pm$ 0.03	0.07 $\pm$ 0.01	0.07 $\pm$ 0.01

Additionally, the native species Hippodamia convergens, Hi. parenthesis, Brachiacantha ursina, Cycloneda munda, Hyperaspis binotata, and Adalia bipunctata were all collected at mean abundances of less than 0.02 in each habitat in 2008.

Table 1.13: Mean $\pm$ SE of coccinellid beetle species found in each field or field margin during 2009. Individual counts were rank transformed and compared using ANOVA. Asterisks (*) indicate a significant difference in abundance between buckwheat strips and control field margins, or between treatment and control fields (**** $p < 0.01$, ** $p < 0.05$, * $p < 0.1$).

Coccinellids	Buckwheat strip	Control field margin		Treatment field	Control field
EXOTIC SPECIES					
<i>Harmonia axyridis</i>	0.31 $\pm$ 0.03	0.27 $\pm$ 0.03		1.07 $\pm$ 0.08	1.09 $\pm$ 0.07
<i>Coccinella septempunctata</i>	1.07 $\pm$ 0.09	0.38 $\pm$ 0.05	***	1.36 $\pm$ 0.08	1.18 $\pm$ 0.07
<i>Hippodamia variegata</i>	0.96 $\pm$ 0.13	0.04 $\pm$ 0.01	***	0.50 $\pm$ 0.05	0.21 $\pm$ 0.02
<i>Propylea quatuordecimpunctata</i>	0.78 $\pm$ 0.08	0.54 $\pm$ 0.05	*	0.71 $\pm$ 0.06	0.71 $\pm$ 0.05
NATIVE SPECIES					
<i>Coleomegilla maculata</i>	0.35 $\pm$ 0.06	0.06 $\pm$ 0.01	***	0.24 $\pm$ 0.03	0.16 $\pm$ 0.02 *

Additionally, the native species *Hippodamia parenthesis*, *Hi. convergens*, *Hi. tredecimpunctata*, *Hi. glacialis*, *Brachiacantha ursina*, *Cycloneda munda*, *Hyperaspis undulata*, *Hy. binotata*, *Hy. proba*, *Hy. bigeminata*, and *Psyllobora vigintimaculata* were all collected at mean abundances less than 0.16 in each habitat 2009.

Table 1.14: Biocontrol Services Index values for aphid suppression by natural enemies for each soybean field in 2008 and 2009.

2008 BSI			2009 BSI		
Site	Treatment	Control	Site	Treatment	Control
Breckenridge	0.993	0.973	Breckenridge	0.846	0.983
Cassopolis	0.901	0.943	Cassopolis	0.991	0.902
Fowlerville	0.948	0.995	Charlotte		0.968
Ithaca	1.000	1.000	Grand Blanc	0.663	0.830
Lapeer	0.990	0.959	Ithaca	0.974	0.927
Leroy	0.972	0.983	Mason	0.985	0.970
Mason	0.932	0.965	Oxford	0.991	0.998
Richfield	0.992	0.958	Silverwood	0.990	0.997
Saginaw	0.976	0.941	Springport	0.995	0.993
Stockbridge	0.776	0.979	Vermontville	0.992	0.983
Vermontville		0.924	Vicksburg	0.943	0.992
Vicksburg	0.922	0.918	Westphalia	0.997	0.968
Average	0.942 $\pm$ 0.002	0.959 $\pm$ 0.008		0.937 $\pm$ 0.031	0.968 $\pm$ 0.008

Figure 1.1: Site locations of paired soybean fields across southern Michigan sampled for aphids and natural enemies in 2008 and 2009. Sites on the same or nearby farms from year to year appear to overlap at this scale (crossed circles), but samples were collected in a different set of fields in each year. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

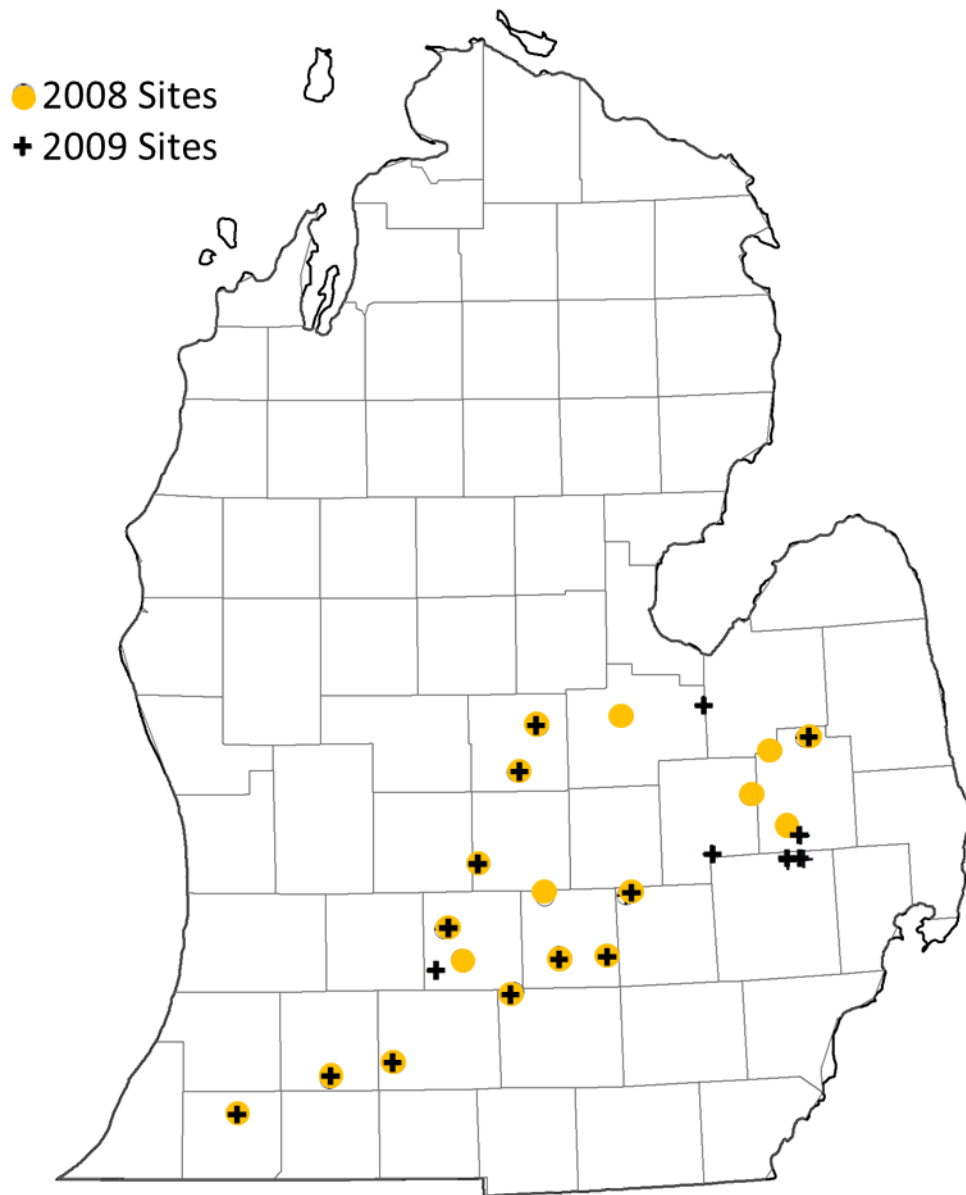


Figure 1.2: Schematic of sampling design showing relative locations of plots and buckwheat strip or control field margin. Inset: a yellow sticky trap and a pair of caged and uncaged soybean plants for the biocontrol experiment were located in the center of each plot.

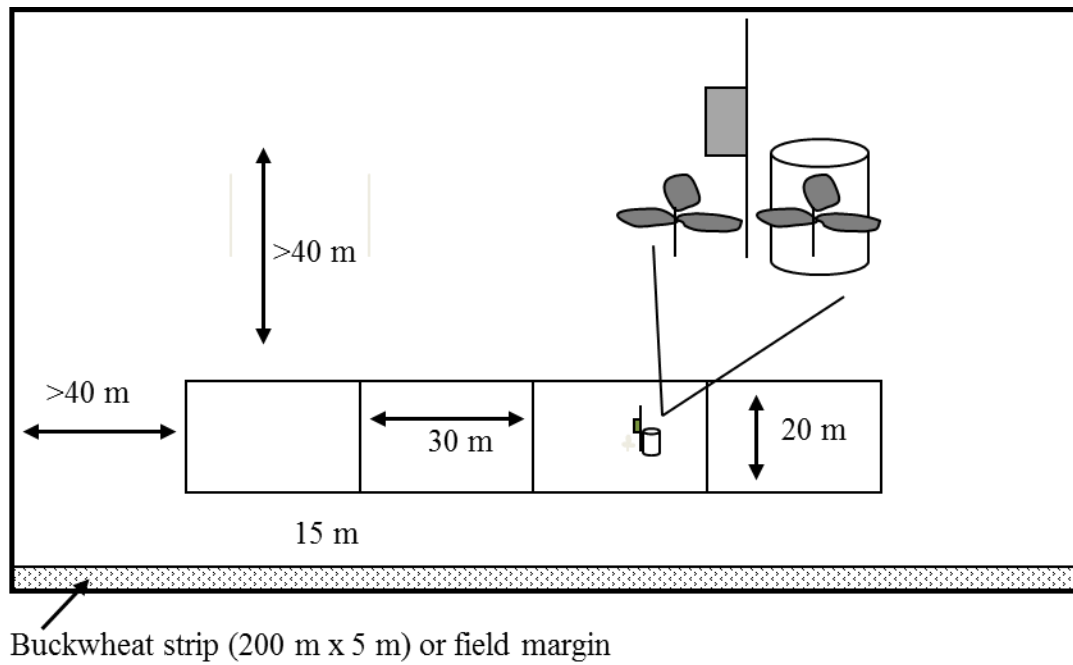


Figure 1.3: An example buckwheat strip in full bloom in July 2009.



Figure 1.4: **A)** Coccinellid abundance in field margins was consistently and significantly higher in buckwheat strips than in control field margins across a gradient of semi-natural habitat within landscapes. **B)** Coccinellid abundance in soybean fields in 2009 increased significantly with the proportion of seminatural habitat in the surrounding landscape at 2.0 km. The effect did not differ between fields adjacent to or without buckwheat strips.

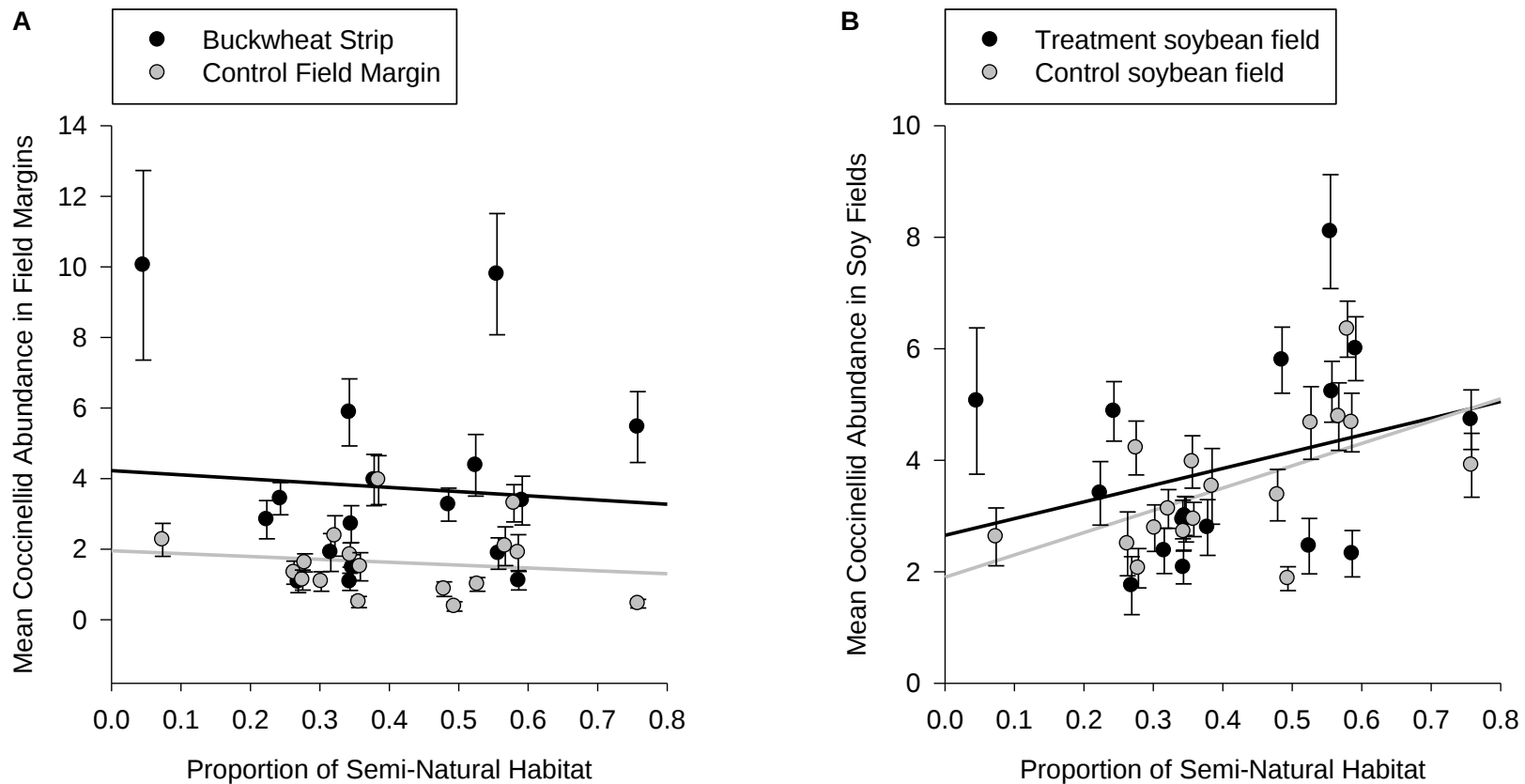
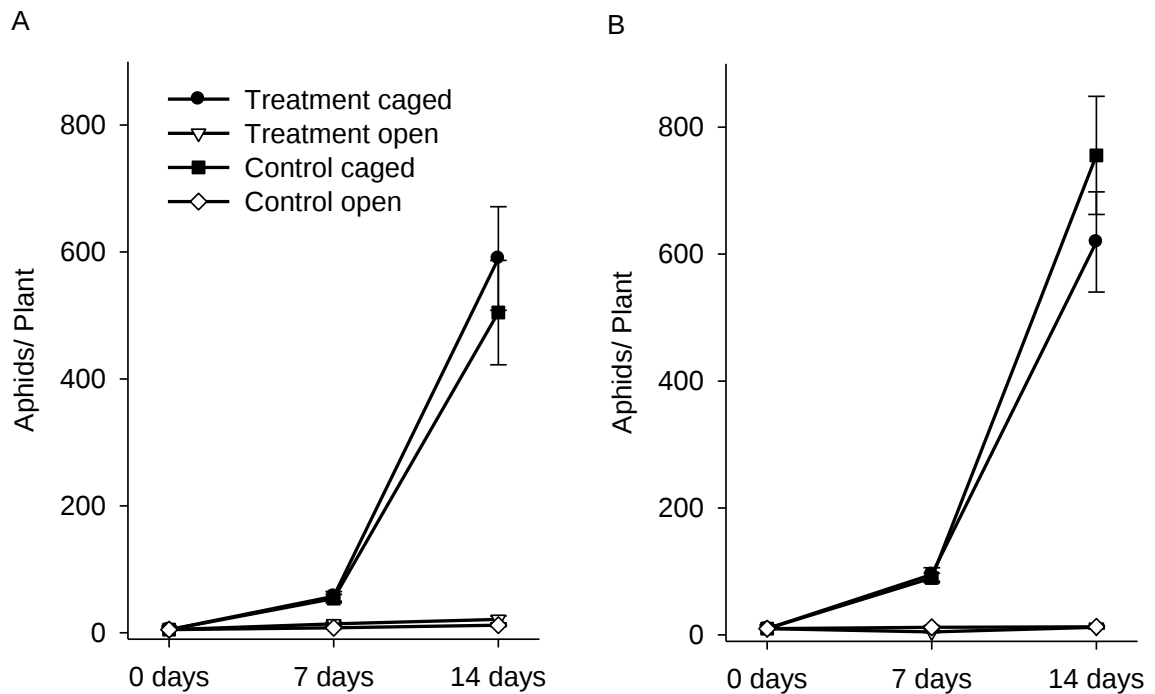


Figure 1.5: Average number of aphids per soybean plant exposed to and excluding predators in treatment and control fields, at 7 and 14 days after infestation in **A) 2008** and **B) 2009**. The horizontal dashed line indicates the economic threshold for soybean aphid of 250 aphids/ plant. In both years, natural enemies dramatically suppressed soybean aphid populations, and the differences in aphid populations between caged and uncaged plants were greater at 14 days than at 7 days. However, buckwheat treatment did not significantly affect the size of the difference in aphid populations on caged and uncaged plants in either year.



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LITERATURE CITED

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CHAPTER II: Coccinellid response to landscape structure across an agricultural intensification gradient.

Abstract

Arthropod natural enemies provide valuable pest suppression in agricultural landscapes, and numerous studies have demonstrated the effects of landscape structure on natural enemy abundance and diversity. In these studies, the amount of semi-natural habitat present in a landscape is frequently used as a proxy for all other aspects of landscape structure. Coccinellid beetles are important generalist predators in a variety of agricultural landscapes. While coccinellids have also been found to be related to the amount of semi-natural habitat in the surrounding landscape, other aspects of landscape structure may be more amenable to management. My goal is to simultaneously assess the effects of landscape composition, including measures of land cover and habitat diversity, and landscape configuration on coccinellid abundances in soybean fields. Here I use Partial Least Squares regression to examine coccinellid response to aspects of landscape structure in more detail. My analyses show that coccinellid abundances were lowest in landscapes dominated by annual crops grown in large fields and highest in landscapes dominated by semi-natural habitat, with a higher diversity of crops grown in smaller fields. My findings suggest a need for studies to separate out potential contributions of these different aspects of landscape structure, especially as some (field size and crop diversity) are more easily managed by growers than semi-natural habitat.

Introduction

Agricultural landscapes cover at least one quarter of terrestrial surfaces on our planet (Millennium Ecosystem Assessment, 2005) and are critical for providing food and fiber for our growing global population. In addition to the production of food and fiber, agricultural landscapes can be managed to produce a variety of ecosystem services, including support of

biodiversity and the regulation of water quality, soil fertility, and greenhouse gases, (Power, 2010; Swinton et al., 2007) and to minimize disservices like soil and nutrient runoff and exposure to pesticides (Power, 2010). Changes in landscape structure influence the provision of these services and disservices. For example, increases in proportional cover of cropland in agricultural landscapes are related to increased pest pressure and insecticide use (Meehan et al., 2011).

Agricultural landscapes also benefit from ecosystem services like pollination and natural pest control (Power, 2010). In the U.S., native and naturalized natural enemies provide pest suppression services to agricultural landscapes worth an estimated \$4.6 billion annually (Losey and Vaughan, 2006). The ultimate success of pest suppression is dependent upon the provision of natural enemies to crop fields by the surrounding landscape. Landscape structure affects the composition of insect communities and the abundance of individual species, which can in turn lead to higher biocontrol rates and less crop damage in more complex landscapes (Thies and Tscharrntke, 1999) and in landscapes with greater proportions of non-crop habitat (Thies et al., 2003).

A number of different metrics have been proposed to quantify landscape structure, including composition metrics that describe which habitats are present and their relative abundances, and configuration metrics that indicate how those habitats are spatially arranged (Turner et al., 2001). Numerous studies have examined the influence of landscape structure on natural enemy communities, yet most of these have focused strictly on landscape composition – specifically, the amount of non-crop or semi-natural habitat (Burel et al., 2013). Semi-natural habitats can provide natural enemies with food resources and shelter during disturbances in crop fields (Bianchi et al., 2006), leading to higher natural enemy abundance (Colunga-Garcia et al.,

1997; Gardiner et al., 2009), species richness (Schmidt et al., 2005) and fecundity (Bommarco, 1998). However, other types of land covers could also influence natural enemy communities. For example, perennial crops may provide many of the same benefits as semi-natural habitat, including reduced disturbance and alternative prey (Landis et al., 2000). Although studies examining perennial crops have been few in number, landscapes which contain more perennial crops have been found to have higher natural enemy activity density (Oberg et al., 2007) and diversity (Elliott et al., 1999), and lower pest rates (Östman et al., 2001).

Habitat diversity, another metric of landscape composition (Turner et al. 2001, McGarigal et al. 2012) may also be important for naturally occurring biological control. Multiple land covers in a local area may provide different resources needed by a single organism (Dunning et al., 1992), which can in turn influence communities in agricultural landscapes (Fahrig et al., 2011). For example, a predatory insect may require one type of habitat for overwintering and another for foraging and egg-laying. As such, habitat diversity within the landscape has also been positively related to natural enemy abundance (Isaia et al., 2006) and to herbivore suppression (Gardiner et al., 2009; Kruess, 2003). Similarly, crop diversity may provide many of the same benefits as overall habitat diversity, as different crops with different phenologies may provide complementary resources at different times of the year (Vasseur et al., 2013).

The influence of landscape configuration, the spatial arrangement of habitats within a landscape, on natural enemies has been largely overlooked in this body of work (Burel et al. 2013). Yet the configuration of habitats can affect the rate of arrival of natural enemies into crop fields (Bianchi et al., 2006), which can in turn influence natural enemy efficacy (Hogg and Daane, 2010). In particular, modeling has shown that an even distribution of non-crop habitats

within a landscape should facilitate colonization of fields by natural enemies (Bianchi and van der Werf, 2003), suggesting that landscapes with small crop fields and greater dispersion of non-crop habitat could promote higher natural enemy abundances in crop fields. Because farmers may have more ability to manipulate some aspects of landscape structure than others, understanding the relationship between these different elements of landscape structure and natural enemy communities has important management implications (Fahrig et al., 2011).

Ladybird beetles (Coleoptera: Coccinellidae) are generalist predators in a variety of agricultural landscapes (Colunga-Garcia et. al, 1997; Obrycki and Kring, 1998). They make a good model taxon to study landscape structure effects because they are known to respond to landscape composition (Gardiner et al., 2009; Woltz et al., 2012), and theoretical models suggest that they should also respond to configuration (Bianchi and van der Werf, 2003). I examined the coccinellid community of soybean fields as part of a separate study examining their efficacy in suppressing soybean aphid, *Aphis glycines* Matsumura, in agricultural landscapes across a gradient of semi-natural habitat (Woltz et al., 2012). Previous work indicates that coccinellids are of primary importance for suppression of soybean aphid (Costamagna and Landis, 2007; Costamagna et al., 2007), the most important insect pest of soybean in the North Central US (Ragsdale et al., 2011). In this study, I assessed the effects of both landscape composition and configuration on coccinellid abundances in soybean fields. I hypothesize that coccinellids will be positively correlated with a) non-crop habitat, b) perennial crops, c) crop diversity, and d) degree of intermixing of crop and non-crop habitat, and negatively correlated with e) annual crop habitats and f) field size. Understanding the relationship between these measures of landscape structure and generalist predators has implications for management of agricultural landscapes globally.

Methods

Site design. This study was replicated in 17 sites across a gradient of landscape diversity in southern Michigan, USA during the summer of 2009 (see Table A.2 in Woltz et al. 2012 for field coordinates). Sites ranged from 6 to 46 km apart, with an average nearest neighbor distance of 23 km. Agriculture in this region consists of a mix of annual field crops (maize, soybean, and wheat) and perennial forage crops (pasture and perennial mixes for hay). Deciduous forests and grasslands or old fields make up the primary non-crop land cover in the area.

Coccinellid counts. Aerially dispersing coccinellids were collected in soybean fields using 22.9 x 27.9 cm unbaited yellow sticky traps (PHEROCON AM, Great Lakes IPM, Vestaburg, MI). Four traps were used in each field, placed 30 m apart from one another and 25 m from a field edge. Field edges were chosen based on ease of access from roads and were distributed among cardinal directions (North n=4; East n=4; South n=7; West n=3 fields). Traps were suspended from step-in plastic fence posts (Woodstream Corporate, Lititz, PA) at plant canopy height and were replaced every week for 8-11 weeks, from 8 June to 26 Aug. All coccinellids captured were identified to species in the field. The number of coccinellids captured per trap per week were used to calculate mean number of coccinellid captures per field.

Landscape data. Ortho-rectified digital aerial photos for each field were obtained from the Michigan Spatial Data Library based on GPS coordinates collected from the center of each field using a handheld GPS receiver. Using these photographs, habitats within a 2.0 km radius around each field were digitized as polygons using ARC GIS 9.3 (ESRI Redlands, CA). For linear patches (e.g. fencerows, roadside vegetation), patches 20 m wide or greater were digitized as distinct habitats. Land cover types and habitat boundaries within field sites were ground-verified, and changes from the aerial photos were noted and corrected during digitization. The

specific land cover within all habitat polygons in each landscape was determined by manually assigning land cover categories to each polygon. The digitized polygon land cover layers for each site were converted to raster format in ARC GIS. The exported rasters were input into Fragstats 4.1 (McGarigal et al., 2012) to calculate landscape metrics (hereafter referred to in italics).

Measures of landscape composition. *Abundance of primary land-covers:* The total area of the three most common crop (*Maize, Soybean, Wheat*) and non-crop (*Grasslands, Forests, Residential areas*) land covers were calculated for each landscape. *Grasslands* included old fields, prairie plantings and Conservation Reserve Program lands (areas planted to “long-term, resource-conserving covers” to provide a variety of ecosystem services (USDA 2013)). *Residential areas* included private residences and public mowed areas like cemeteries and municipal parks. Small woodlots were included in the *Forest* total. Additionally, the abundance of pasture, alfalfa, orchard grass, and other forage crops were calculated and combined into a single variable, *Forage crops*, representing perennial agricultural crops.

Cover diversity: Simpson’s Diversity Index (*SDI*) (Simpson, 1949) was used as a metric of landscape heterogeneity (McGarigal et al., 2012). This index is less sensitive than other diversity measures to the number of land cover types because *SDI* is based on the proportion of area that each habitat type constitutes rather than the absolute area, and rare habitats will contribute smaller proportions (Magurran, 2004). Therefore, it effectively describes the variance in relative abundances of habitat types without being skewed by the presence of rare habitats (Magurran, 2004). Overall habitat diversity within the landscape, $SDI_{habitat}$, was calculated using the proportional cover of every land cover type identified in ground-truthing using the formula:

$$SDI = 1 - \sum p_i^2,$$

where p_i = proportion of landscape occupied by patch type i . This formulation of the index varies from 0 to 1 and can be intuitively interpreted as the probability that any two randomly chosen pixels are of different composition.

In addition to overall habitat diversity ($SDI_{habitat}$), I also calculated crop diversity (SDI_{crop}) using the proportion of every crop type identified. These two metrics were not highly correlated with one another ($r^2 = 0.01$) and could represent two different pools of resources for natural enemies.

Measures of landscape configuration. *Crop mesh size:* I calculated an effective mesh size ($MESH$) using only crop land covers, to represent average field size in each landscape, according the formula:

$$MESH = \sum \sum a_{ij}^2 / A,$$

where a_{ij} is the area of patch ij (m^2), and A is the total landscape area (m^2) (McGarigal et al., 2012). $MESH$ is a metric of average size (ha) of landscape patches. Thus, landscapes with larger crop $MESH$ values have fewer, larger fields and landscapes with smaller $MESH$ values have more, smaller fields.

Landscape shape index: I re-coded the landscape maps identifying each patch as either crop or non-crop and calculated a Landscape Shape Index (LSI),

$$LSI = 0.25E^* / \sqrt{A},$$

where 0.25 is an adjustment for raster data, E^* is the total length of edge in the landscape in meters, including the borders of all patches identified during digitization. A is the total area of the landscape in square meters (McGarigal et al., 2012). LSI is greater than or equal to 1, with one indicating a landscape comprised of one large patch. LSI increases as the amount of edge in the landscape increases. LSI is a measure of both the total amount of edge existing between land covers of different types and of habitat aggregation. As a particular land cover becomes more dispersed throughout a landscape, the amount of edge increases. Thus, higher LSI values represent landscapes with greater dispersion of crop and non-crop habitat, while lower LSI values represent landscapes in which crop and non-crop habitats are aggregated into larger patches.

Statistical analyses. I used a Partial Least Squares (PLS) regression approach (PROC PLS SAS 9.2) to model variation between the landscape variables and mean coccinellid abundance. The goal of PLS is to extract underlying factors, consisting of linear combinations of predictor variables that account for variation in predictor and response variables. PLS analyses can handle multiple, highly correlated predictor variables (Wold et al., 2001) making it more flexible than the more commonly used multiple linear regression, in which correlated predictor variables lead to unstable parameter estimates. Using PLS regression allows us to consider the relationship between multiple correlated landscape variables, instead of using semi-natural habitat as a proxy for all the others, as has been done in the past (Burel et al., 2013).

PLS regression algorithms extract factors that account for the greatest amount of variation in predictor and response variables simultaneously. While PLS is closely related to Principal Components Analysis (PCA), in PCA factors are chosen that explain the most variation in predictor variables independently of response variables, regardless of whether those factors are relevant to the predictors (Abdi, 2010). Additionally, PLS can handle data sets in which there

are more predictor variables than observations (Carrascal et al., 2009). While PLS has been most commonly used in econometrics and chemistry, the ability to analyze datasets in which there are a large number of correlated predictor variables and a relatively small sample size makes this method quite useful for ecological studies (Carrascal et al., 2009). For example, Rusch and colleagues (2012) used PLS to examine landscape influences on the abundance of pollen beetles (*Meligethes aeneus* F.).

It is common practice to transform predictor and response variables to achieve symmetry prior to conducting PLS regression (Wold et al., 2001). I used a Shapiro-Wilk statistic to determine if variables were symmetrical. I square-root transformed proportions of *Wheat*, *Forage crops*, *Residential areas* and *Grasslands*, as well as *MESH*, and cubed $SDI_{habitat}$ and repeated Shapiro-Wilk tests to confirm that symmetry (normality) had been achieved. Results using the transformed and untransformed datasets were almost identical, and I report the results from the transformed data set to conform with standards in the published literature (Wold et al. 2001).

Data were centered to a mean of zero and scaled to a standard deviation of 1 to give each variable equal weight in the analysis (Wold et al., 2001). I used one-at-a-time cross-validation to determine the appropriate number of factors to extract from the data. In this technique, one observation is removed and the model is fit with the remaining observations and used to predict the missing observation. The difference between the actual and predicted value for the missing observation is calculated. This procedure is repeated for each observation in the data set and the sum of squares for the error from each model is used to calculate the predicted residual sum of squares (PRESS). PRESS is analogous to the residual sum of squares in regular regression and is an indicator of the model's predictive power. To select the appropriate number of factors for a

given model, first multiple orthogonal factors are estimated that are each linear combinations of the predictors variables. Each subsequent factor explains less of the overall variation in the response and predictor variables. In the cross-validation procedure, the PRESS is calculated separately for models with different numbers of factors, and the model that minimizes PRESS is chosen as the best. Because in some cases a model with more factors may have only slightly lower PRESS, I used Van der Voet's test to determine if models with fewer extracted factors had insignificantly higher PRESS at a 10% level (SAS Institute Inc., 2011).

After the appropriate number of factors was selected, I assessed the model's goodness of fit by examining R^2_X , R^2_Y , and Q^2 . R^2_X is the amount of variation in the matrix of predictor variables that the model explains, R^2_Y is the amount of variation in the matrix of response variables that the model explains, and Q^2 is the amount of variation in the response variable that the model predicts through the cross-validation procedure. I then plotted the loadings of predictor and response variables for each factor to look for curvature or outliers, and examined the coefficients and variable influence on projection (VIP) values to for each variable to determine the contribution of each variable to the model (Wold et al., 2001). Variables with low VIP values (below 0.80) and regression coefficients near zero have little influence on the response variable and make little contribution to the structure of the overall PLS model (SAS Institute Inc., 2011).

Results

Coccinellid captures. In 11 weeks of sampling, I captured a total of 1,989 coccinellids. Average captures per trap per week ranged from 1.9 to 6.4 coccinellids/trap. The coccinellid community within soybean fields was dominated by exotic coccinellids, with *Coccinella*

septempunctata making up 33%, *Harmonia axyridis* 31%, *Propylea quatuordecimpunctata* 20%, and *Hippodamia variegata* 6%, of all coccinellids captured. The most common native coccinellids captured were *Coleomegilla maculata* and *Hippodamia parenthesis*, making up 5 and 3% of total captures. Other species made up 1% or less of captures.

Landscape variables. Landscapes represented a gradient from agriculturally-dominated to forest-dominated. *Soybean*, *Maize*, *Forest*, and *Residential areas* had the biggest ranges across landscapes, while *Grasslands*, *Forage crops*, and *Wheat* had smaller gradients (Table 2.1). These 7 main composition variables combined made up 79.6 to 99.4% of all landscapes studied.

$SDI_{habitat}$ and SDI_{crop} had similar ranges, although they were not correlated with one another. The range in *MESH* indicated a gradient of landscapes with average crop fields of roughly 1 to 84 ha (Table 2.1).

In addition to the three most common annual crops and forage crops, several other crops were identified in the studied landscapes in lower abundances, which also contribute to crop diversity, SDI_{crop} . These included: dry beans (comprising a maximum of 8.1% of all landscapes studied), non-wheat small grains (e.g. barley, oats; 2.2%), sugar beets (1.9%), clover cover crop (1.5%), vegetables (0.3%) and fruit trees (0.1%). Additionally, although alfalfa, orchard grass, and pastures were grouped as forage crops, they were included separately in crop diversity calculations, each contributing a maximum of 8.1, 6.1, and 6.0 % of landscapes, respectively.

PLSR model. The model with one extracted factor had the lowest PRESS, and the PRESS was significantly lower than the model with zero factors ($p < 0.04$). Factor 1 explained 51.7% of variation in the landscape predictor variables (R^2_X) and 63.8% of variation in mean

coccinellid abundances (R^2_Y). Furthermore, the model with one factor explained 51.2% of the variation in mean coccinellid abundance (Q^2).

The plot of response and predictor scores from factor 1 shows a linear positive relationship between response and predictor scores and indicates no outliers, grouping of data, or curvature in this relationship (Figure 2.1). Residual plots for response and predictor variables indicate no heterogeneities.

Factor 1 primarily explains a gradient from landscapes dominated by a few annual crops grown in large individual fields to landscapes with higher crop diversity, smaller fields, and more abundant non-crop habitats. Mean coccinellid abundance, SDI_{crop} , and the abundance of *Grasslands*, *Forests*, and *Residential areas* load positively with factor 1, while *MESH* (average field size) and the abundance of *Maize*, *Soybean* and *Wheat* load negatively (Figure 2.2). The variables *Grassland* and *Residential area* have the highest correlation with mean coccinellid abundance. The variables *Forage* and $SDI_{habitat}$ had low Variable Importance for Projection (VIP; Table 2.1) and regression coefficients near zero, indicating that they were not important in structuring factor 1. All other variables had greater influence on the structure of the model (e.g. VIP variables > 0.8 ; Table 2.1). The model explained moderate amounts of variation in the proportion of wheat in the landscape and LSI, and 60-80% of variation in the other variables.

Because variables with low VIP and coefficients close to zero have little influence on the model, it is common to delete them and rerun the PLS to obtain a better PLS model for predictive purposes (SAS Institute Inc., 2011). Rerunning the model without $SDI_{habitat}$ and

Forage increased the R^2_X to 62.5%, but other results (i.e. R^2_Y , Q^2 , VIP values, residual plots) were nearly unchanged.

Discussion

Naturally occurring pest suppression from native or naturalized natural enemies is an important ecosystem service in crop production (Losey and Vaughan, 2006; Swinton et al., 2006). This study showed that both landscape composition and configuration may influence the abundance of a group of important generalist predators. Landscapes in this study represented a range of agricultural intensification typical of the upper Midwestern U.S., with landscapes dominated by semi-natural habitat and having high crop diversity and small crop field size at one end of the gradient and landscapes dominated by a few annual crops grown in large fields at the other.

Mean summer coccinellid abundance in soybean fields increased with increasing non-crop cover in the landscape. Similar positive effects of non-crop habitat on predator and parasitoid abundances have been found in a variety of systems, including canola, wheat and cotton (Prasifka et al., 2004; Schmidt and Tschardtke, 2005; Thies and Tschardtke, 1999). Non-crop habitat could have contributed to increased coccinellid abundances by providing resources such as overwintering habitat, nectar and pollen, and alternative hosts and prey (Bianchi et al., 2006).

However, because it is unlikely that many farmers will remove substantial amounts of land from production to increase non-crop area, it is also useful to consider the benefits of aspects of landscape structure more under farmer control, such as crop type, overall crop diversity, and field size. In this study, the diversity of crops grown in the landscape and mean coccinellid abundance both loaded strongly positively with factor 1, which explained a gradient

from landscapes dominated by a few annual crops to those with more natural habitat, higher crops diversity, and smaller field sizes. Crop diversity could be important for natural enemies because resources in one crop may become available as resources in another crop are diminishing, due to differing crop phenologies (Vasseur et al., 2013). Surprisingly, I did not find a relationship between perennial forage crops and coccinellid abundance. This may be because coccinellids correlated strongly along an agricultural intensification gradient, while perennial forage crops were grown in both agriculturally dominated and non-crop dominated landscapes.

The negative relationship between average crop field size and coccinellid abundance may suggest that coccinellids are more likely to colonize small fields. In landscapes with smaller fields, more soybean area will be adjacent to edges shared with other cover types (Bianchi et al., 2006), which could provide food and refuge resources to coccinellids. Furthermore, the increased area of cover type interfaces allows increased arrival rates of dispersing coccinellids from other cover types into soybean (Bianchi and van der Werf, 2003). Alternatively, the relationship between field size and coccinellids could be an artifact of landscape change and the association between coccinellids and crop cover. In this region, the landscapes in which the most maize and soybean are grown tend to have fertile soils and flat, well-drained land, allowing these crops to be grown in larger fields.

Contrary to my hypothesis, I found an inverse relationship between *LSI* and coccinellids. This may be the result of correlations between *LSI* and other variables that are stronger drivers of coccinellids abundance. For example, coccinellids are highly correlated with the amount of non-crop habitats. In this set of landscapes, greater amounts of non-crop habitat tends to be aggregated into larger patches of grassland or forest, which would lead to having lower *LSI* values. Therefore, the strong effect of non-crop habitat on coccinellids could be driving this

counter-intuitive relationship. Alternatively, the fact that coccinellids are strong fliers might negate the influences of landscape configuration in this system. It would be informative to conduct a similar study measuring a suite of natural enemies with different dispersal abilities, to determine if the strength of configuration effects increase as dispersal abilities decline.

I have shown several landscape factors that are strongly related to both coccinellid captures in soybean fields and to each other. Such correlations among landscape variables are common, making it difficult for researchers to assert causal relationships. For example, many studies of landscape influences on natural enemies and biological control use semi-natural habitat as their primary measure of landscape structure, using it as a proxy for habitat diversity and citing the strong correlation between these two variables in their studies (Roschewitz et al., 2005; Steffan-Dewenter et al., 2002; Thies and Tschardtke, 1999). Notably, in this study, overall habitat diversity was not strongly correlated with any of the non-crop land covers. Instead, I found overall habitat diversity was highest at intermediate ranges of non-crop habitat, and had low explanatory value in the model. This example highlights the need for caution when drawing conclusions about the influences of a particular landscape variable on natural enemies, particularly when there are legitimate hypotheses for why multiple landscape factors may be involved. Studies which carefully select landscapes that vary independently in key landscape variables may be particularly informative; however, that may be easier in theory than practice (Fahrig et al., 2011).

Conclusions

There is growing evidence that crop pest populations cannot be effectively managed without consideration of landscape influences (Cumming and Spiesman, 2006; Schellhorn et al., 2008). Understanding the influence of landscape composition and configuration on natural

enemy abundance and movement in agroecosystems is one prerequisite to such region-wide pest management. Given that farmers may have more control over their crop selection and field size than over semi-natural habitat surrounding their farms, future studies to isolate these aspects of landscape structure will be necessary to move forward on landscape-scale pest management. Additionally, given that landscapes dominated by annual crop covers are likely to experience not only greater pest pressure but also increased insecticide use (Meehan et al., 2011; O'Rourke and Jones, 2011), a broad understanding of the relationship between landscape structure and natural pest suppression is critical for mitigating potential ecosystem disservices in agricultural landscapes.

APPENDIX

Chapter II Tables and Figures

Table 2.1: Landscape variables used in PLS analysis organized by variable type. Variables analyzed are shown in *italics*. Minimum and maximum values for each variable within the studied landscapes are shown, along with variable influence for project (VIP) values. R^2_x indicates the percent of variation in each predictor variable explained by Factor 1.

COMPOSITION	min.	max.	VIP	R^2_x
Primary Land Covers (%):				
Annual crops:				
<i>Soybean</i>	4.8	39.7	1.15	65.0
<i>Maize</i>	0.4	47.2	0.85	60.5
<i>Wheat</i>	0.0	15.6	1.05	45.4
<i>Forage crops</i> ¹	0.4	14.7	0.10	0.1
Non-crop:				
<i>Forest</i>	2.4	64.7	0.85	63.1
<i>Residential</i>	1.9	29.5	1.35	73.3
<i>Grasslands</i>	3.5	14.8	1.35	59.2
Cover diversity				
<i>SDI_{habitat}</i>	0.57	0.85	0.35	7.8
<i>SDI_{crop}</i> ²	0.76	1.00	1.10	78.4
CONFIGURATION				
<i>MESH</i>	0.94	83.98	1.15	80.1
<i>Landscape Shape Index</i>	3.25	7.55	0.85	35.8

¹*Forage crops* consist of pasture, alfalfa, orchard grass and other crops grown for hay

²In addition to the crops listed above, the amount of dry beans, small grains, sugar beets, clover, vegetables and fruit trees were included in crop diversity calculations.

Figure 2.1: Relationship between coccinellid abundance in soybean fields in 2009 and landscape variable scores from PLS analysis. Predictor and explanatory variables show a positive correlation within factor 1, suggesting that this factor captures a real relationship between these variables.

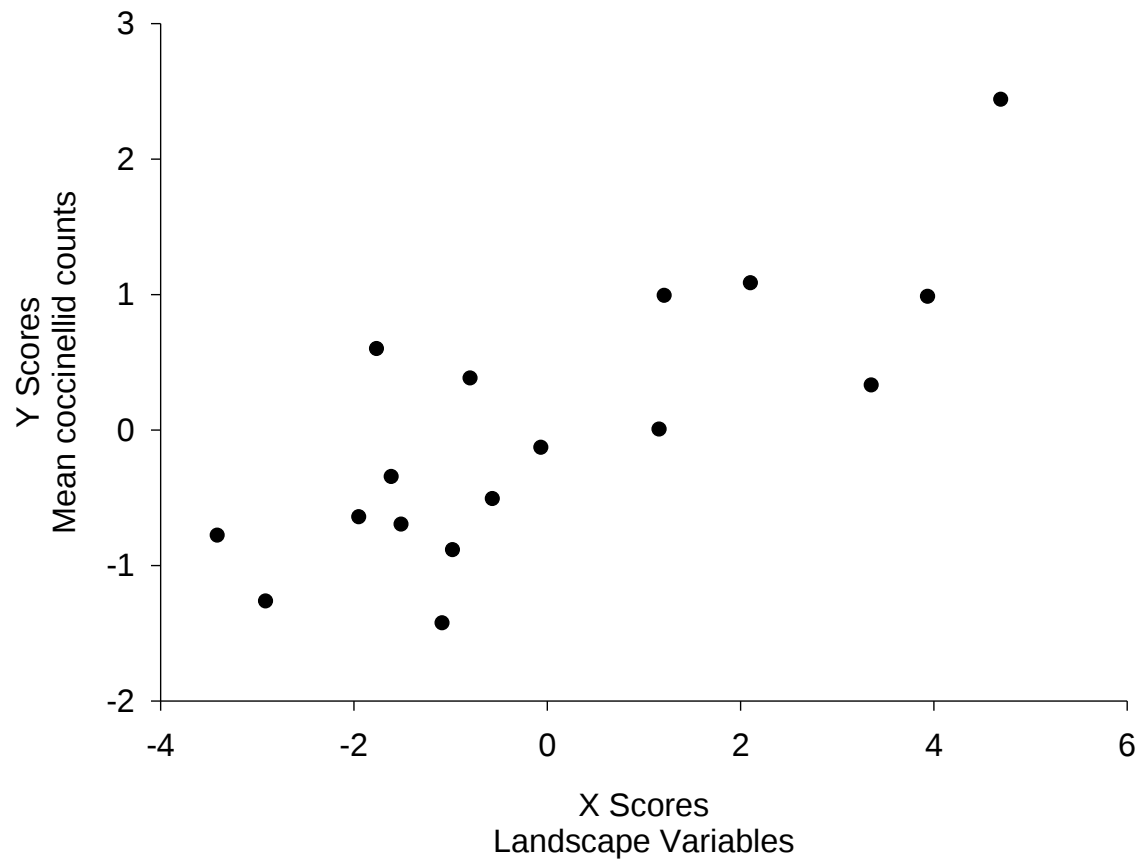
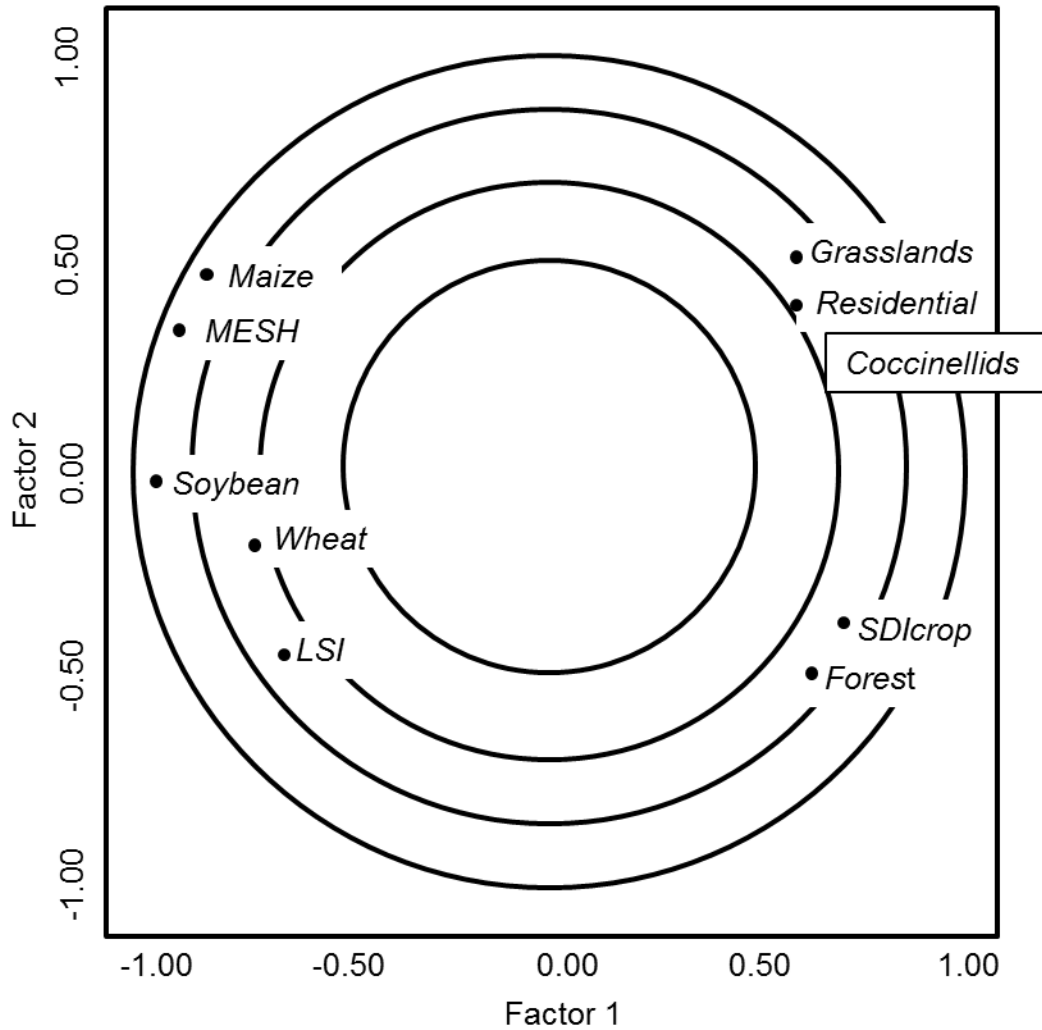


Figure 2.2: Loadings of response (coccinellids, in box) and predictor (landscape) variables from PLS regression. The abundance of coccinellids loads positively along factor one, along with non-crop habitats like *grasslands*, *residential areas*, and *forests*, and with crop diversity (SDI_{crop}). In contrast, annual crops (*maize*, *soybean*, *wheat*) and crop field size (*MESH*) load negatively. The numbers 1 through 17, representing the landscapes, are generally spread-out and show no obvious outliers.



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LITERATURE CITED

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CHAPTER III: Coccinellid immigration to infested host patches influences suppression of *Aphis glycines* in soybean.

Woltz, J.M. and D.A. Landis, 2013. Coccinellid immigration rate influences suppression of *Aphis glycines* in soybean. *Biological Control*. 64: 330-337.

Abstract

Generalist natural enemies may be well adapted to annual crop systems in which pests and natural enemies re-colonize fields each year. In addition, for patchily-distributed pests, a natural enemy must also disperse within a given crop field to arrive at infested host patches. As they typically have long generation times compared to their prey, theory suggests that generalist natural enemies need high immigration rates both to and within fields to effectively suppress pest populations. The soybean aphid, *Aphis glycines* Matsumura, is a pest of an annual crop and is predominantly controlled by coccinellids. To test if rates of coccinellid arrival at aphid-infested patches are crucial for soybean aphid control, we experimentally varied coccinellid immigration to 1m² soybean patches using selective barriers and measured effects on *A. glycines* population dynamics. In a year with low ambient aphid pressure, naturally-occurring levels of coccinellid immigration to host patches were sufficient to suppress aphid population growth. In contrast, decreasing coccinellid immigration rates resulted in large increases in soybean aphid populations within infested patches. Activity of other predatory taxa was very low in this year, suggesting that most of the differences in aphid population growth were due to changes in coccinellid immigration. Alternatively, in a year in which alate aphids continually colonized plots, aphid suppression was incomplete and increased activity of other predatory taxa contributed to adult coccinellid predation of *A. glycines*. Our results suggest that in a system in which natural enemy

populations cannot track pest populations through reproduction alone, immigration of natural enemies to infested patches can compensate for reproduction rates and result in pest control.

Introduction

Natural enemies of crop pests exhibit a wide range of life history traits that influence their effectiveness as biological control agents. Modeling studies suggest that effective pest suppression may be obtained from either specialist natural enemies inflicting high mortality rates, or from generalist natural enemies with high immigration rates into an infested area (Chang and Kareiva, 1999). Additionally, each of these strategies may be better adapted to particular crop types. For example, specialist natural enemies may be well-adapted for perennial crops in which temporal stability allows equilibrium to be achieved between natural enemy and pest populations, while generalists may be better suited for annual crops which both pests and natural enemies have to recolonize each growing season (Murdoch et al., 2006). Furthermore, because generalist natural enemies like coccinellids (Coleoptera: Coccinellidae) tend to have long generation times relative to those of their prey and thus cannot rapidly respond numerically to pest population dynamics (Dixon et al., 1997; Kindlmann and Dixon, 1999a; Kindlmann and Dixon, 1999b; Kindlmann and Dixon, 2001), generalists must exhibit high immigration rates to be effective (Murdoch et al., 2006). In fact, higher immigration rates have been demonstrated to decrease the predator/ prey ratios necessary for effective pest suppression (van der Werf, 1995), and manipulating immigration rates of generalist predators has resulted in lower pest abundance and higher yields (Snyder and Wise, 1999).

Natural enemy immigration occurs at different temporal and spatial scales. In annual agriculture, many natural enemies overwinter outside of the crop and must first immigrate into crop fields after their establishment. Once in the crop habitat, they must then disperse and locate

prey-infested patches within the field. In this manuscript, we focus on the process of patch-level immigration and its impact on populations of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), an invasive and economically damaging pest of soybean (*Glycines max* (L.) Merrill).

In the north central U.S., soybean is typically grown in annual rotation with other crops and both *A. glycines* and many of its natural enemies must colonize the crop each season (Ragsdale et al., 2011). Furthermore, because *A. glycines* is patchily distributed in soybean fields (Costamagna and Landis 2011), it is necessary for predators to locate and immigrate to aphid-infested patches within soybean fields. In North America, generalist predators provide the majority of natural control of *A. glycines*, and multiple studies indicate that if predators are reduced or excluded entirely, *A. glycines* quickly reach outbreak levels (Brosius et al., 2007; Costamagna and Landis, 2006; Costamagna et al., 2007; Desneux et al., 2006; Donaldson et al., 2007; Fox et al., 2005; Gardiner et al., 2009; Rhainds et al., 2007; Schmidt et al., 2007). Large, mobile predators play a particularly important role in *A. glycines* suppression. Both Gardiner and Landis (2007) and Costamagna and others (2008) showed that small, less mobile predators like *Orius insidiosus* (Say) and various predatory larvae were unable to control *A. glycines*, while aphid populations were significantly lower when they were accessible by large predators like coccinellids. Furthermore, the large coccinellid beetles *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas have been shown to be highly efficient *A. glycines* predators, having the highest per capita consumption rate of the *A. glycines* predators studied to date, and contribute to a majority of *A. glycines* predation in the North Central U.S. (Costamagna and Landis, 2007). In addition, these two species are dominant in soybean fields in Michigan. *H.*

axyridis and *C. septempunctata* together accounted for 75 and 62 % of total lady beetle captures in Michigan soybean fields in 2008 and 2009 (Woltz, unpub. data).

Most coccinellid beetles have long generation times relative to aphids, suggesting an inability to suppress aphid prey through reproduction alone (Dixon et al., 1997; Kindlmann and Dixon, 1999a; Kindlmann and Dixon, 1999b; Kindlmann and Dixon, 2001). Furthermore, although *H. axyridis* and *C. septempunctata* over-wintered adults are active in spring foraging in crops like alfalfa and wheat (Colunga-Garcia and Gage, 1998; LaMana and Miller, 1996), there is very little production of larvae in soybean fields before mid-summer when *A. glycines* populations are rapidly increasing. This is because coccinellids require minimum prey densities to oviposit (Seagraves, 2009), tend to oviposit near aphid colonies, and lay more eggs when more prey are available (Hodek and Honek, 1996). For example, in surveys of 34 soybean fields throughout the soybean-producing region of Michigan in 2009, lady beetle larvae were not detected in soybean fields until 20 July even though aphids were present by the first week of June (Woltz unpub. data). Thus, we predict that early-summer predation of *A. glycines* on small soybean plants due to adult coccinellids regularly arriving at and predating aphid-infested patches within soybean fields will be crucial to overall *A. glycines* suppression.

Here, we measure the importance of patch-level coccinellid immigration for suppressing aphid populations by experimentally varying coccinellid immigration to 1 m^2 soybean patches by using selective barriers. We hypothesize that: 1) our manipulations would create a gradient of coccinellid immigration within the plots and that 2) decreases in early summer growing season lady beetle immigration would result in increases in aphid populations within plots.

Methods

Site. This study was conducted during the summers of 2010 and 2011 on and around the Kellogg Biological Station, Long Term Ecological Research Site (KBS LTER; 42.405714 N, 85.377658 W). Agriculture in this region consists of a mix of annual field crops (corn, soy, and wheat) and perennial forage crops (pasture and perennial mixes for hay). Deciduous forests and old field successions make up the primary non-crop land cover in the area. Study fields were planted between 10 and 24 May in 2010 and between 9 May and 2 June in 2011. Sampling took place weekly from 16 June to 9 July in 2010, and 5 to 26 July in 2011. Sampling was later in 2011 because a rainy spring delayed soybean herbicide applications in this region and thus our access to fields. During the first week of the 2010 experiment, soybean plants ranged from the two to five trifoliate growth stage (V2-5) (Higley and Boethel, 1994), while during the first week of the 2011 experiment, soybean plants ranged from the four to six trifoliate growth stage (V4-6).

Plot establishment. This study was replicated in $n=8$ soybean fields in each year. Each field contained three treatment types manipulating patch-level immigration, crossed with two sampling types for a total of 6 plots per field and 48 plots per year. Predators and *A. glycines* were monitored in 1 x 1 m plots in which the immigration of coccinellids to host patches was differentially manipulated by use of selective barriers. Selective cages and barriers can be used to manipulate the movement of key coccinellids through plots without altering levels of other predators or abiotic conditions (Costamagna et al., 2007; Gardiner and Landis, 2007; Gardiner et al., 2009). In a previous experiment, we observed that 1 m x 1 m plots surrounded by four-sided 40 cm tall polyethylene plastic fences (i.e. fully open tops) reduced the number of adult coccinellids entering the plot. This occurred even though prey density was significantly higher

on plants inside of plots (Landis and van der Werf, 1997). Upon encountering such vertical barriers, adult coccinellids frequently climb upward to the top edge, and typically initiate a short flight (D. Landis pers. obs.). While some subsequently land inside the enclosed plot, many do not, and thus even simple barriers can be used to manipulate the density of transient adult coccinellids. Plots were placed at least 10 m from the edge of each field and a minimum of 20 m from other plots. Coccinellids are strong fliers capable of dispersing long distances (Hodek et al., 1993). In our previous studies, we have found that coccinellids in soybean fields are captured on sticky traps at similar rates at distances of 25, 50, and 100 m away from field edges. Therefore, the distance of our treatment plots from the field edge or from each other should not influence the potential numbers of coccinellids entering each plot. The same design was used in each field, and barrier treatments and sampling types were randomly assigned to each location. Plots were centered on a soybean row such that each contained 3 rows of soybean plants grown 38.1 cm apart. All fields received commercial levels of fertilizer and weed control but no insecticides were applied.

Three treatments were used to manipulate coccinellid immigration within the 1 m x 1 m plots (Figure 3.1). The “open” treatment had no barriers to immigration of coccinellids, and plot corners were simply demarcated with stakes. In a second treatment, “2-sided” barriers were erected on opposite sides of the plot, blocking immigration from those two sides while leaving the top and other sides open. A 1m³ PVC frame was erected around each plot and secured into the soil. The east and west facing sides of the 1m³ frame were wrapped in coarse mesh netting (2 mm openings) that allowed smaller predators to pass through, but prevented coccinellids from entering (Costamagna et al., 2007). The mesh extended from the top of the frame sides to 2 cm above the ground, allowing ground-dwelling predators (Carabidae, Araneae, etc.) to freely enter

and exit the plots (Figure 3.1). The effect of wind on coccinellid flight is debated (Hodek and Honek, 1996). At our site the dominant wind direction is west to east, thus our barriers consistently blocked coccinellids traveling with or against the wind irrespective of row orientation. Finally, in a third treatment, “5-sided,” the 1 m³ PVC frame was covered on all four sides and the top with coarse mesh netting (2 mm openings) also raised 2 cm above the ground, blocking coccinellid immigration from all directions. Previous research has shown little or no effect of predator exclusion cages on microclimate within cages (Fox et al., 2004; Hopper et al., 1995; Schmidt et al., 2003), little or no effect of cages on soybean growth (Fox et al., 2004), biomass, or yield (Costamagna et al., 2008), and little or no effects on soybean aphid growth separate from changes in predator density (Costamagna et al., 2008; Fox et al., 2004).

Each field contained two sets of each treatment. One set used as “sampling plots” in which predators were sampled without replacement. The other set was used as “observation plots” in which aphid populations were monitored. This allowed us to eliminate any effects of predator removal on aphid abundance. At the initiation of the experiment, every soybean plant in each plot was visually inspected and all insects found were removed.

Predator monitoring. To determine the efficacy of our barrier treatments for manipulating immigration to plots, coccinellids and other aerially-dispersing predators (chrysopids (Neuroptera: Chrysopidae), hemerobeids (Neuroptera: Hemerobedidae), lampyrids (Coleoptera: Lampyridae), cantharids (Coleoptera: Cantharidae), and dolichopodids (Diptera: Dolichopodidae)) were measured within sampling plots with 23 x 28 cm unbaited yellow sticky cards (PHEROCON AM, Great Lakes IPM, Vestaburg, MI). All coccinellids on the cards were counted and identified to species in the field. The traps were placed in the center of each sampling plot suspended from step-in plastic fence posts at plant canopy height and were

replaced weekly (Figure 3.1 A-C). We also measured activity-density of ground-dwelling predators to test our assumption that they would not be affected by the barrier treatments. Ground-dwelling predators including carabids (Coleoptera: Carabidae), staphylinids (Coleoptera: Staphylinidae), elaterids (Coleoptera: Elateridae), formicids (Hymenoptera: Formicidae), spiders (Araneae) and harvestmen (Opiliones), were collected in 11 cm diameter pitfall traps filled with 1:1 propylene glycol: water solution. Pitfall traps were collected and reset each week. Foliar-dispersing predators, those residing on the foliage and likely to disperse short distances from plant to plant, were assessed with weekly visual plant surveys. Each week the 5 plants surveyed for aphids within each plot were also inspected for syrphid larvae (Diptera: Syrphidae), coccinellid larvae, chrysopid eggs and larvae, and anthocorid (Hemiptera: Anthocoridae) adults and nymphs.

Aphid monitoring. Naturally occurring aphid populations within each study field were monitored weekly using whole plant counts. During the first week of sampling, the centermost plant in all plots was infested with 10 greenhouse-reared (2010) or field-collected (2011) aphids of mixed age classes representing natural incipient colonies. Aphid abundances were counted weekly on the infested plant and on 4 additional randomly selected plants within each plot. Apterous and alate aphids were counted separately to account for the different modes in which aphid populations could be increasing in the plots. Briefly, aphid densities can increase through reproduction, triggering the production of large numbers of winged alate dispersal morphs. Alternatively, the appearance of alate aphids at low aphid densities suggests the arrival of new colonizers from other infested patches, fields, or hosts. Plot counts were stopped after 4 (2010) or 5 (2011) weeks due to a build-up of alates in the 5-sided treatment.

Aphid populations within fields were monitored weekly by randomly placing a 1m² quadrat within the soybean field. Five quadrat samples were taken each week in each field. Five random plants within each quadrat were inspected for apterous and alate *A. glycines*, coccinellid adults and larvae, lacewing larvae, syrphid larvae, and anthocorid adults and nymphs. The vegetative growth stage of each surveyed plant was determined according to Higley and Boethel (1994) and recorded. Finally, the number of soybean plants within each quadrat was recorded.

Statistical analysis. For all of the insect taxa, neither data nor residuals were normal and variance was heterogenous and increased with the mean. Therefore, insect data were analyzed using generalized linear models, which estimate parameters with less bias than modeling transformed data (O'Hara and Kotze, 2010) and avoid complications of making inferences in the untransformed scale (Venables and Ripley, 2002). We analyze data for each taxon separately for each year. Soybean aphid dynamics are known to vary dramatically from year to year (e.g. Rhainds et al., 2010) and we did not wish to average over this important variation. We report results for all tests for which levels are different at $\alpha < 0.1$, using Tukey's adjustment for multiple comparisons.

Predator counts: The activity-density of coccinellids, lampyridae (2011 only), six taxa of ground-dwelling predators (formicids, carabids, staphylinids, elaterids, spiders, and harvestmen), and anthocorids (2011 only), were analyzed using separate generalized linear mixed models (PROC GLIMMIX; SAS 9.2). With the exception of anthocorids, individuals per trap for each taxon were modeled with a negative binomial distribution, a common distribution for over-dispersed count data. Data from each year were analyzed separately. The lognormal distribution was the best fit for the average number of anthocorids (combined adults and nymphs) per plant in each plot in 2011, the only foliar-dispersing predator abundant enough to analyze statistically.

Other predator taxa were not captured frequently enough to allow for statistical comparisons between treatments. Captures rates for all taxa (untransformed mean $\pm$ s.e.) are summarized in the results.

For each taxon we analyzed statistically, we treated treatment, week and their interaction as fixed effects and field as a random block. Laplace estimation was used to estimate means and Wald F- and t-tests were used for hypothesis testing (Bolker et al., 2009). Least square means comparisons were constructed on the linked scale. Because of difficulty in model convergence for coccinellid data, non-significant effects were dropped from the model and least square means comparisons were run on models containing only significant effects.

Aphid abundance: Aphid counts from observation and sampling plots were modeled with a negative binomial distribution using a repeated measures generalized linear model (PROC GENMOD; SAS 9.2). Plot was the subject of the repeated measures across weeks. Repeated measures were used in the case of aphid abundance because we followed the same population of aphids within a plot over time. In contrast, predator data were drawn from random samples of the broader population and are not expected to be correlated from week to week. Data from each year were analyzed separately.

Results

Adult coccinellid captures. A total of 231 and 355 adult coccinellids were collected on sticky traps in 2010 and 2011. Four exotic and five native species of adult coccinellids were captured in both years (Tables 3.1, 3.2). Three exotic species accounted for 84 and 85 % of all coccinellids collected in 2010 and 2011, respectively. *H. axyridis* accounted for 38 and 47 %, *P. quatuordecimpunctata* accounted for 34 and 20 %, and *C. septempunctata* accounted for 11 and 18 %. No other coccinellid species accounted for more than 6 % of total captures in either year.

We successfully manipulated adult coccinellid immigration into plots in both years. In 2010, adult coccinellid immigration into plots differed by treatment ($F_{2,103} = 2.82$, $p=0.06$; Figure 3.2), but not by week ($F_{3,103}=1.02$, $p=0.39$), and the treatment by week interaction was not significant ($F_{6,103}=0.65$, $p=0.69$). Trap catches averaged 3.1 ± 0.41 coccinellids per week in the open treatment, 2.1 ± 0.40 coccinellids per week in the 2-sided treatment, and 0.42 ± 0.24 in the 5-sided treatment. There were significantly more adult coccinellids in the open treatment than in 5-sided treatments ($t_{112}=6.79$, $p<0.0001$), and significantly more in 2-sided than in 5-sided ($t_{112}=5.77$, $p<0.0001$). There was a trend toward higher adult coccinellid captures in open than in 2-sided plots, but this difference was not significant at Tukey-adjusted levels. The three most common species followed these patterns of having captures in the open, intermediate in the 2-sided, and lowest in the 5-sided plots (Tables 3.1, 3.2).

In 2011 adult coccinellid immigration into plots differed by treatment ($F_{2,84} = 8.01$, $p=0.0007$; Figure 3.2), but not by week ($F_{3,84}=1.30$, $p=0.28$), and the treatment by week interaction was not significant ($F_{6,84}=0.57$, $p=0.75$). There were 6.03 ± 1.04 adult coccinellids in the open treatment, 2.38 ± 0.33 in the 2-sided treatment, and 0.26 ± 0.10 in the 5-sided treatment. There were significantly more adult coccinellids in the open treatment than in 2-sided ($t_{86}=4.16$, $p<0.0001$) or in 5-sided ($t_{86}=7.43$, $p<0.0001$), and significantly more in 2-sided than in 5-sided ($t_{86}=5.50$, $p<0.0001$).

Ground-dwelling predators. Average captures for each ground-dwelling taxon are shown in Table 3.3. Of the six taxa examined, only carabidae varied between treatments in 2010

($F_{2,99}=3.13$, $p=0.05$). Carabids were captured more frequently in 5-sided than in two-sided plots ($t_{99}=2.48$, $p=0.04$). Captures in open plots were intermediate to the 5- and 2-sided plots and not statistically different from either. Several taxa varied between weeks (Formicidae: $F_{3,99}=14.13$, $p<0.0001$; Carabidae: $F_{3,99}=3.36$, $p=0.02$; Staphylinidae: $F_{3,99}=20.27$, $p<0.0001$; Elateridae: $F_{3,99}=10.01$, $p<0.001$; Opiliones: $F_{3,99}=2.53$, $p=0.06$), generally increasing over time. No taxon showed a significant week by treatment interaction in 2010.

Only Carabidae and Opiliones varied between treatments in 2011 ($F_{2,98}=3.92$, $p=0.02$; $F_{2,98}=6.60$, $p=0.002$, respectively). Carabids were captured more frequently in 5-sided than open plots ($t_{98}=2.76$, $p=0.02$). Captures in 2-sided plots were intermediate to the 5-sided and open plots and not statistically different from either. Opiliones were captured more frequently in both 5- and 2-sided plots than in open plots ($t_{98}=3.06$, $p=0.008$; $t_{98}=3.39$, $p=0.003$, respectively), but did not differ between 5- and 2-sided plots. Spiders, opiliones, formicids and staphylinids varied between weeks ($F_{4,98}=3.89$, $p=0.006$; $F_{4,98}=14.02$, $p<0.0001$; $F_{4,98}=10.96$, $p<0.0001$; $F_{4,98}=5.61$, $p=0.0004$, respectively). Captures of all five of these taxa increased and decreased erratically between weeks, with no consistent patterns. Additionally, there was a significant week X treatment interaction for formicids in 2011 ($F_{8,98}=2.21$, $p=0.03$), although no differences in treatments were consistent over time, and no individual comparisons were significant using adjusted p-values.

Foliar- and aerially-dispersing predators. Most foliar-dispersing predators were found in low abundances with no systematic differences between treatments (Table 3.4). Anthocorids in 2011 did not vary by week ($F_{3,122}=2.16$, $p=0.10$) or by treatments ($F_{2,122}=2.11$, $p=0.13$). However, there were significant interaction effects ($F_{6,122}=2.67$, $p=0.02$). There were more anthocorids per plant in two-sided than in the open treatment in week 2 ($t_{122}=2.17$, $p=0.03$). In week three, there were more anthocorids per plant in both open and two-sided than in the 5-sided treatment ($t_{122}=2.03$, $p=0.04$; $t_{122}=3.68$, $p=0.0003$, respectively).

Lampyrids in 2011 varied by week ($F_{4,98}=6.53$, $p=0.0001$) and treatment ($F_{2,98}=24.25$, $p<0.0001$) but there was no interactive effect ($F_{8,98}=1.43$, $p=0.19$). There were more lampyrids captured in the open treatment than in either the 2- or 5-sided treatment ($t_{98}=5.10$, $p<0.0001$; $t_{98}=5.54$, $p<0.0001$, respectively). Other aerially-dispersing predators were collected in fairly low numbers relative to coccinellid captures, and in general, were highest in the open treatment and lowest in the 5-sided treatment (Table 3.5).

Aphid abundance. In 2010, natural aphid pressure in the study fields was very low, never reaching more than 1.72 aphids / plant in any field in any week. Within infested plots, aphid numbers varied between treatment ($\chi^2_2=109.02$, $p<0.0001$), week ($\chi^2_3=98.23$, $p<0.0001$), and their interaction ($\chi^2_6=142.47$, $p<0.0001$). All plots had the same number of aphids when infested, with treatment differences developing over time (Figure 3.3). In the first week there were no differences between aphid counts. In week 2 there were significantly more aphids in both 5-sided and 2-sided treatments than in the open treatment ($\chi^2_1=7.65$, $p=0.006$; $\chi^2_1=4.22$,

$p=0.04$, respectively), but not between 5- and 2-sided. In week 3, all treatments had significantly different numbers of aphids. In week 4, there were significantly more aphids in the 5-sided treatment than in both the open and 2-sided treatments, but no difference between open and 2-sided treatments. By the fourth week, there were 105 ± 38 aphids/ plant in the 5-sided treatment, but only 7 ± 3 aphids/ plant in 2-sided treatments and 3 ± 1 aphids/ plant in the open treatment.

In 2011, aphids within the treatment plots increased over each week ($\chi^2_3=1319.91$, $p<0.0001$), but there were no differences by treatment ($\chi^2_2=2.31$, $p=0.31$) and no interactive effects ($\chi^2_6=6.50$, $p=0.37$). However, in 2011 arrival of alate aphids in fields was higher than in 2010 (Figure 3.3). In 2010, no naturally colonizing alate aphids were observed in any soybean fields, although there was some build-up of alatae in 2- and 5-sided treatments during weeks 3 and 4 (Table 3.6). In 2011, however, naturally-colonizing alatae were observed in every week, and were found in all treatments from week 2 on (Table 3.6).

Discussion

We set out to determine if the patch-level immigration of adult coccinellids influenced aphid suppression in soybean fields. Our treatments were effective at creating a range of coccinellid immigration to local host patches. In both years there were significantly fewer coccinellids captured in 5-sided than open treatments, with captures in 2-sided treatments intermediate to these. Lampyrids were also captured at higher rates in open than 2- or 5-sided plots. However, lampyrids are expected to make limited contributions to soybean aphid suppression because their capture rates in soybean fields tend to be lower than coccinellids, they are considered to be somewhat specialized predators of earthworms and snails (Debach and Rosen, 1991), and they have never been confirmed to feed on soybean aphid despite numerous

surveys of predators in North American soybean fields (Ragsdale et al., 2011). In contrast to coccinellids and lampyrids, activity-density of other predatory taxa was not consistently influenced by treatment (e.g. anthocorids), was highest in the 5-sided treatment (e.g. opiliones and carabids), or was low in comparison to coccinellid activity-density.

Changing the patch-level immigration rate of coccinellids altered *A. glycines* dynamics, as populations showed trends toward higher numbers in the plots with the lowest coccinellid captures in both years. Aphid populations were highest in the 5-sided treatment in spite of increased activity-density of some ground-dwelling predators in these plots. Increased opiliones and carabid activity-densities in 5-sided plots may be a result of aggregation to higher prey resources as the bottoms of treatment barriers were open and allowed free access to these predators.

There are several possible explanations for the different aphid dynamics in 2010 and 2011 despite similar coccinellid immigration rates into the different treatment plots for the first three weeks of each year of the study. In both years, aphid populations in the open and two-sided plots remained similar to ambient levels in the surrounding soybean fields. A steady influx of alate aphids from the surrounding field or landscape into the plots in 2011 could be responsible for weekly population increases within the plots. Few alates were found in 2010, and only in plots with high densities of aphids, suggesting that these alates were produced within those plots, as aphids typically produce dispersal morphs in response to crowding (Dixon, 1985). In contrast, in 2011 alates were found in our treatment plots and in the surrounding field in every week after our initial infestation, even in plots with low densities of aphids, suggesting that these alates represented additional migrants to the plots. The reproduction of the alates within our plots would have boosted populations beyond what would be expected from reproduction from our

original 10 aphids alone. Additionally, while the abundance of foliar-dispersing predators was low and variable in both years, abundances were generally higher in 2011. The increase of these predators across all treatments in 2011 may have contributed to the lack of significant differences in aphid populations in this year, while helping to hold populations in all treatments below economic threshold. However, due to their low consumption rates (Costamagna and Landis, 2007), it is unlikely that these foliar-dispersing predators such as *Orius insidiosus* and coccinellid and chrysopid larvae were primarily responsible for *A. glycines* suppression in either year. Finally, the higher captures of opiliones and carabids in 5- and 2-sided plots in 2011 may have offset reductions in coccinellid immigration into these two treatment plots and be at least partially responsible for the lack of significant differences in aphid abundance between the treatments in this year. One species of opiliones has been observed feeding on soybean aphid in North America (Allard and Yeargan, 2005) and nine species of carabids captured in soybean fields fed on soybean aphid in laboratory no-choice trials (Hajek et al., 2007; Hannam et al., 2008; Rutledge et al., 2004).

Coccinellid captures on sticky traps were within the range typically seen in Michigan soybean fields (e.g. Woltz et al., 2012). With low ambient aphid populations in the field in 2010, a coccinellid immigration rate of approximately 2 – 3 individuals captured in a plot per week was sufficient to prevent *A. glycines* population increase in both open and 2-sided treatments. This seemingly low activity-density of coccinellids implies that high numbers of coccinellids are not necessary to suppress soybean aphid populations if individuals are regularly moving through and predating in aphid-infested patches. In a study of the spatial dynamics of soybean aphid infestations in soybean fields, Costamagna and Landis (2011) found that areas of high *Aphis glycines* density in one week typically became areas of low density in subsequent weeks,

suggesting that predators regularly located patches with increasing aphid density and drove populations back to average field levels. In contrast, in a year like 2011 with higher external aphid pressure from alates regularly colonizing soybean fields, coccinellid immigration alone may not be sufficient to counter the influx of new aphids and aphid densities may rise. Under such conditions, the densities of foliar-dispersing predators such as anthocorids and coccinellid and chrysopid larvae are likely to increase, increasing their contribution to aphid suppression. The changing roles of various predators under different levels of ambient aphid pressure is an interesting question that warrants further study.

Previous studies have shown that adult coccinellids aggregate in patches of high prey density (Hodek and Honek, 1996), a behavior resulting from decreased emigration from host patches (Krivan, 2008). However, for patches with low aphid densities, we have shown that the immigration of coccinellid beetles to aphid infested patches is important for *A. glycines* suppression. Similar results have been found in other systems. For example, experimentally decreasing carabid and lycosid immigration into squash plots resulted in higher pest densities and lower squash yield (Snyder and Wise, 1999). Furthermore, although coccinellid emigration from a patch is related to characteristics such as prey density, the presence of potential predators or competitors, immigration into a patch is random with respect to the quality of that patch (Krivan, 2008). Rather, rates of immigration into a particular patch are determined by coccinellid decisions to leave nearby patches (Grez and Prado 2000) as well as their overall densities in the landscape. Because coccinellid immigration rates to patches within soybean fields should be higher when their overall density in the landscape is higher, management actions to increase coccinellid immigration to aphid colonies must take place outside of the crop. Increasing evidence suggests that landscape composition at scales of multiple kilometers influences the

activity-density of coccinellids in crop fields, likely because the presence and abundance of particular habitats determines the provision of resources necessary for coccinellid survival and reproduction (Gardiner et al., 2009; Woltz et al., 2012).

APPENDIX

Chapter III Tables and Figures

Table 3.1: Means $\pm$ standard errors for all adult coccinellid species captured on sticky traps in 2010.

	2010		
	0	2	5
EXOTIC SPECIES			
<i>Harmonia axyridis</i>	1.275 $\pm$ 0.277	0.700 $\pm$ 0.249	0.184 $\pm$ 0.184
<i>Coccinella septempunctata</i>	0.350 $\pm$ 0.122	0.275 $\pm$ 0.134	0
<i>Propylea quatuordecimpunctata</i>	1.000 $\pm$ 0.238	0.725 $\pm$ 0.175	0.211 $\pm$ 0.086
<i>Hippodamia variegata</i>	0.050 $\pm$ 0.035	0.050 $\pm$ 0.035	0
NATIVE SPECIES			
<i>Cycloneda munda</i>	0.125 $\pm$ 0.053	0.150 $\pm$ 0.067	0
<i>Coleomegilla maculata</i>	0.200 $\pm$ 0.073	0.125 $\pm$ 0.053	0.026 $\pm$ 0.026
<i>Brachiacantha ursina</i>	0.075 $\pm$ 0.042	0.025 $\pm$ 0.025	0
<i>Hippodamia parenthesis</i>	0.050 $\pm$ 0.035	0.050 $\pm$ 0.035	0
<i>Hi. convergens</i>	0	0	0

Table 3.2: Means $\pm$ standard errors for all adult coccinellid species captured on sticky traps in 2011.

	2011		
	0	2	5
EXOTIC SPECIES			
<i>Harmonia axyridis</i>	3.450 $\pm$ 0.757	0.675 $\pm$ 0.191	0.026 $\pm$ 0.026
<i>Coccinella septempunctata</i>	1.275 $\pm$ 0.293	0.325 $\pm$ 0.083	0.026 $\pm$ 0.026
<i>Propylea quatuordecimpunctata</i>	0.800 $\pm$ 0.130	0.900 $\pm$ 0.171	0.077 $\pm$ 0.043
<i>Hippodamia variegata</i>	0.275 $\pm$ 0.107	0.075 $\pm$ 0.042	0.026 $\pm$ 0.026
NATIVE SPECIES			
<i>Cycloneda munda</i>	0.225 $\pm$ 0.091	0.200 $\pm$ 0.073	0.051 $\pm$ 0.036
<i>Coleomegilla maculata</i>	0.050 $\pm$ 0.035	0.100 $\pm$ 0.060	0.051 $\pm$ 0.051
<i>Brachiacantha ursina</i>	0.050 $\pm$ 0.035	0.050 $\pm$ 0.035	0
<i>Hippodamia parenthesis</i>	0.075 $\pm$ 0.042	0.025 $\pm$ 0.025	0
<i>Hi. convergens</i>	0.050 $\pm$ 0.034	0.025 $\pm$ 0.025	0

Table 3.3: Means $\pm$ standard errors for the most common ground-dwelling predator species captured in pitfall traps in 2010 and 2011.

	Carabidae	Elateridae	Staphylinidae	Formicidae	Spiders	Opiliones
<i>2010</i>						
open	4.925 $\pm$ 1.035	1.450 $\pm$ 0.716	7.725 $\pm$ 1.799	9.250 $\pm$ 1.812	15.325 $\pm$ 2.403	9.700 $\pm$ 1.239
2-sided	3.800 $\pm$ 1.016	1.200 $\pm$ 0.731	11.075 $\pm$ 3.094	7.000 $\pm$ 1.371	11.600 $\pm$ 2.079	10.575 $\pm$ 3.152
5-sided	8.275 $\pm$ 1.894	0.525 $\pm$ 0.193	10.200 $\pm$ 2.421	6.950 $\pm$ 1.757	9.000 $\pm$ 1.512	10.575 $\pm$ 3.152
<i>2011</i>						
open	4.350 $\pm$ 0.602	0.525 $\pm$ 0.179	3.400 $\pm$ 0.724	18.300 $\pm$ 1.687	17.050 $\pm$ 2.471	4.750 $\pm$ 1.247
2-sided	5.500 $\pm$ 0.781	1.075 $\pm$ 0.466	3.675 $\pm$ 0.578	22.700 $\pm$ 4.389	18.775 $\pm$ 3.349	6.225 $\pm$ 1.037
5-sided	8.650 $\pm$ 1.673	0.875 $\pm$ 0.355	6.750 $\pm$ 1.860	16.225 $\pm$ 2.927	20.700 $\pm$ 3.984	6.475 $\pm$ 1.159

Table 3.4: Means $\pm$ standard errors for foliar-dispersing predators observed on soybean plants in 2010 and 2011.

	Syrphid larvae	Coccinellid larvae	Anthocorid adults	Anthocorid nymphs	Chrysopid larvae
<i>2010</i>					
open	0.031 ± 0.011	0.006 ± 0.004	0.006 ± 0.004	0.028 ± 0.011	0.006 ± 0.004
2-sided	0.088 ± 0.043	0.003 ± 0.003	0.006 ± 0.004	0.009 ± 0.005	0.016 ± 0.008
5-sided	0.250 ± 0.105	0.003 ± 0.003	0.016 ± 0.007	0.019 ± 0.011	0.013 ± 0.006
<i>2011</i>					
open	0.005 ± 0.004	0.038 ± 0.010	0.103 ± 0.028	0.346 ± 0.040	0.035 ± 0.013
2-sided	0.003 ± 0.003	0.038 ± 0.013	0.113 ± 0.022	0.533 ± 0.055	0.020 ± 0.009
5-sided	0	0.020 ± 0.007	0.110 ± 0.036	0.333 ± 0.037	0.058 ± 0.017

Table 3.5: Means $\pm$ standard errors for aerially-dispersing predator species captured on sticky traps in 2010 and 2011.

	Coccinellidae	Chrysopidae	Hemerobeidae	Lampyridae	Cantharidae	Dolichopodidae
<i>2010</i>						
open	3.125 ± 0.405	0.200 ± 0.089	0.100 ± 0.100	1.150 ± 0.575	0.075 ± 0.042	0.125 ± 0.064
2-sided	2.100 ± 0.398	0.300 ± 0.103	0.075 ± 0.042	0.300 ± 0.114	0.050 ± 0.035	0
5-sided	0.421 ± 0.243	0.079 ± 0.044	0	0.132 ± 0.086	0	0
<i>2011</i>						
open	6.025 ± 1.041	0.075 ± 0.042	0.075 ± 0.042	3.800 ± 0.712	0.075 ± 0.055	1.000 ± 0.275
2-sided	2.375 ± 0.330	0.075 ± 0.042	0.025 ± 0.025	1.200 ± 0.249	0	0.375 ± 0.106
5-sided	0.256 ± 0.095	0.026 ± 0.026	0.026 ± 0.026	1.051 ± 0.345	0	0.128 ± 0.066

Table 3.6: Average number of alate aphids observed per plant in each week in each plot in 2010 and 2011.

2010				
week	field	open	2	5
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0.025 ± 0.025
4	0	0	0.050 ± 0.039	4.675 ± 4.178
5	0	0	---	---
6	0	---	---	---
7	0	---	---	---
8				
2011				
week	field	open	2	5
1	0.385 ± 0.112	0	0	0
2	0.060 ± 0.022	0.100 ± 0.042	0.088 ± 0.044	0.088 ± 0.044
3	0.040 ± 0.016	0.063 ± 0.027	0.025 ± 0.018	0.013 ± 0.013
4	0.060 ± 0.018	0.013 ± 0.013	0.025 ± 0.018	0
5	0.141 ± 0.036	0.225 ± 0.073	0.063 ± 0.027	0.200 ± 0.156
6	0.135 ± 0.025	---	---	---
7	0.085 ± 0.026	---	---	---
8	0.217 ± 0.044	---	---	---

Figure 3.1: Predator activity-density and aphid abundance were measured in 1 m² plots. Barriers to coccinellid immigration were constructed with 2 mm opening mesh netting and were raised 2 cm above the ground to allow full access by small and ground-dwelling predators. Open plots (A & D) had no barriers to immigration. 2-sided plots (B & E) had barriers erected on the east and west sides of plot. 5-sided plots (C & F) had barriers on all sides. Each field contained two sets of plots. In sampling plots (A-C), predators were sampled without replacement. In observation plots (D-F), aphid populations were monitored without disturbing predator populations.

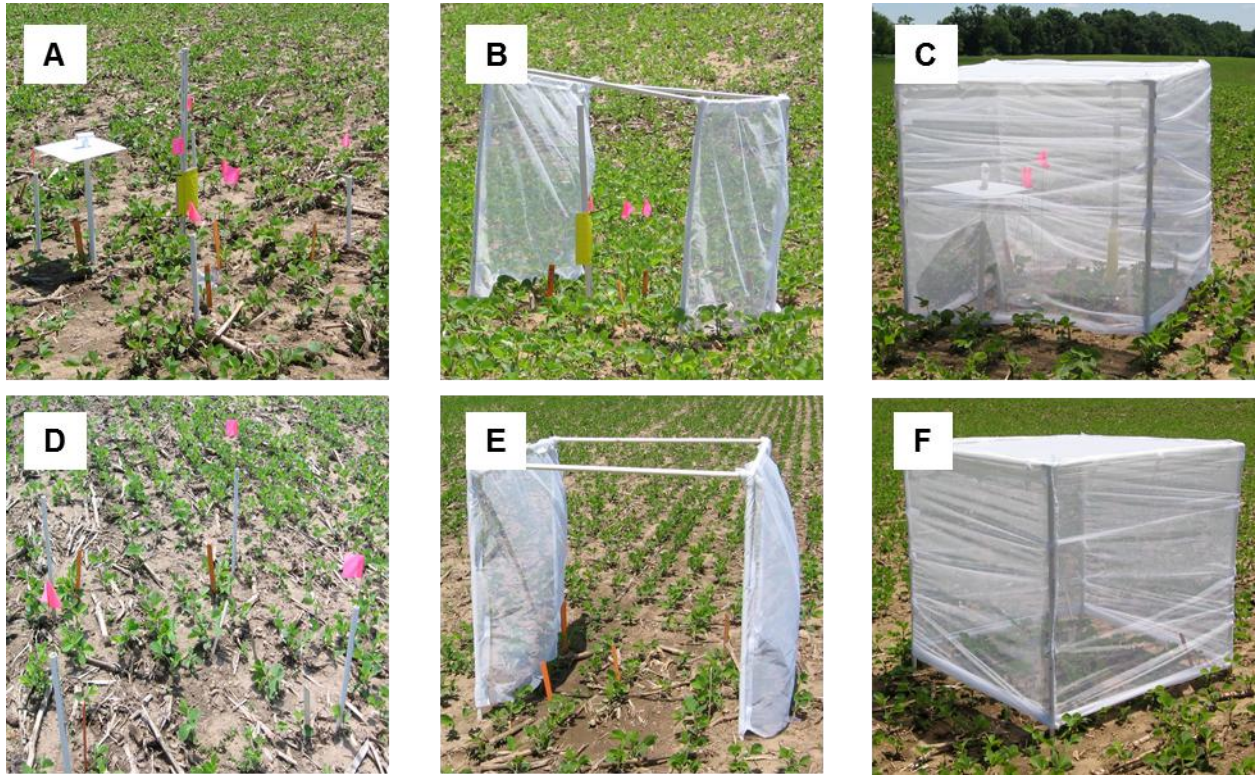


Figure 3.2: Mean number of adult coccinellids captured in treatment plots in 2010 and 2011. In 2010, coccinellid immigration was higher in open and 2-sided than in 5-sided treatment plots. In 2011, coccinellid immigration rates were different in all treatments.

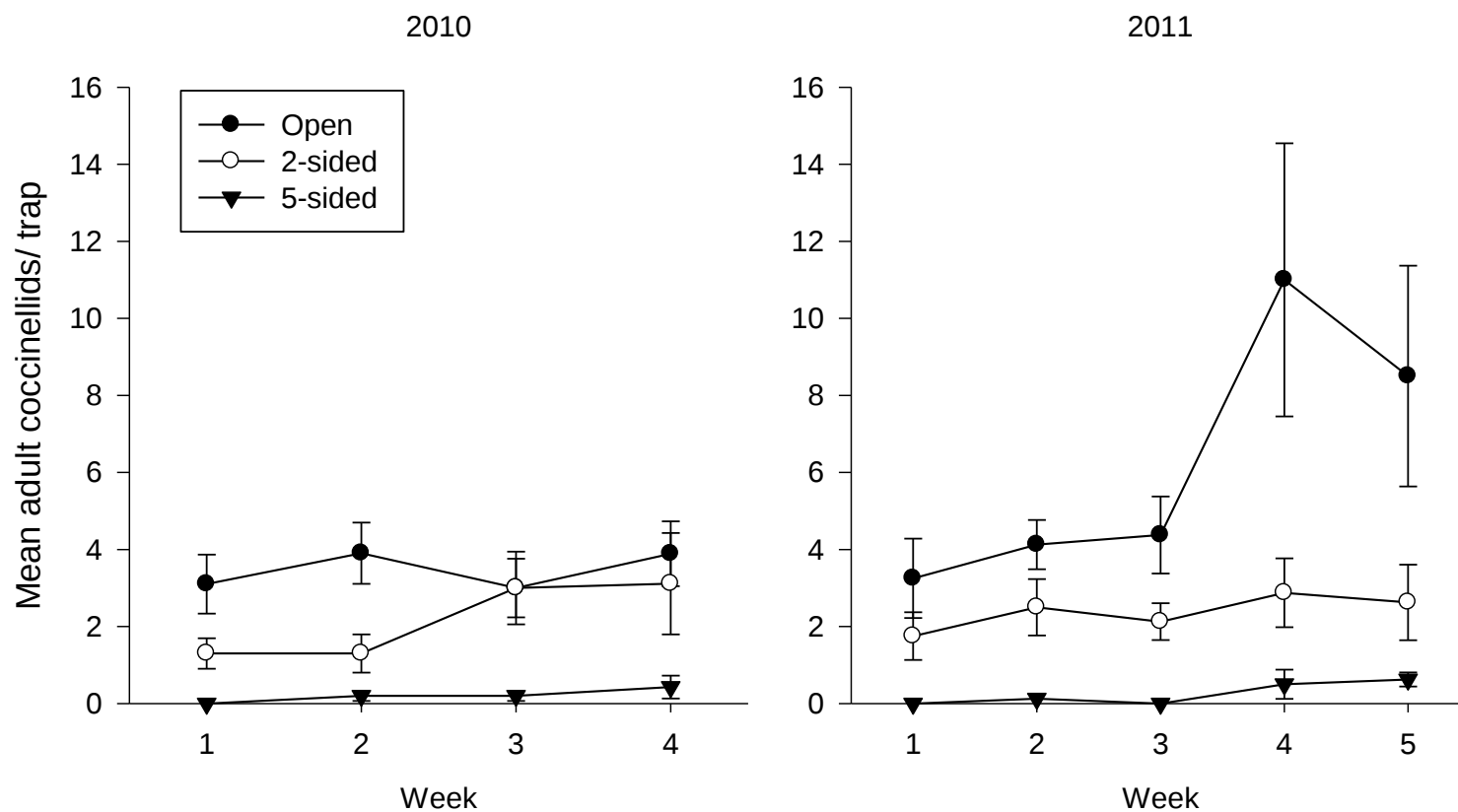
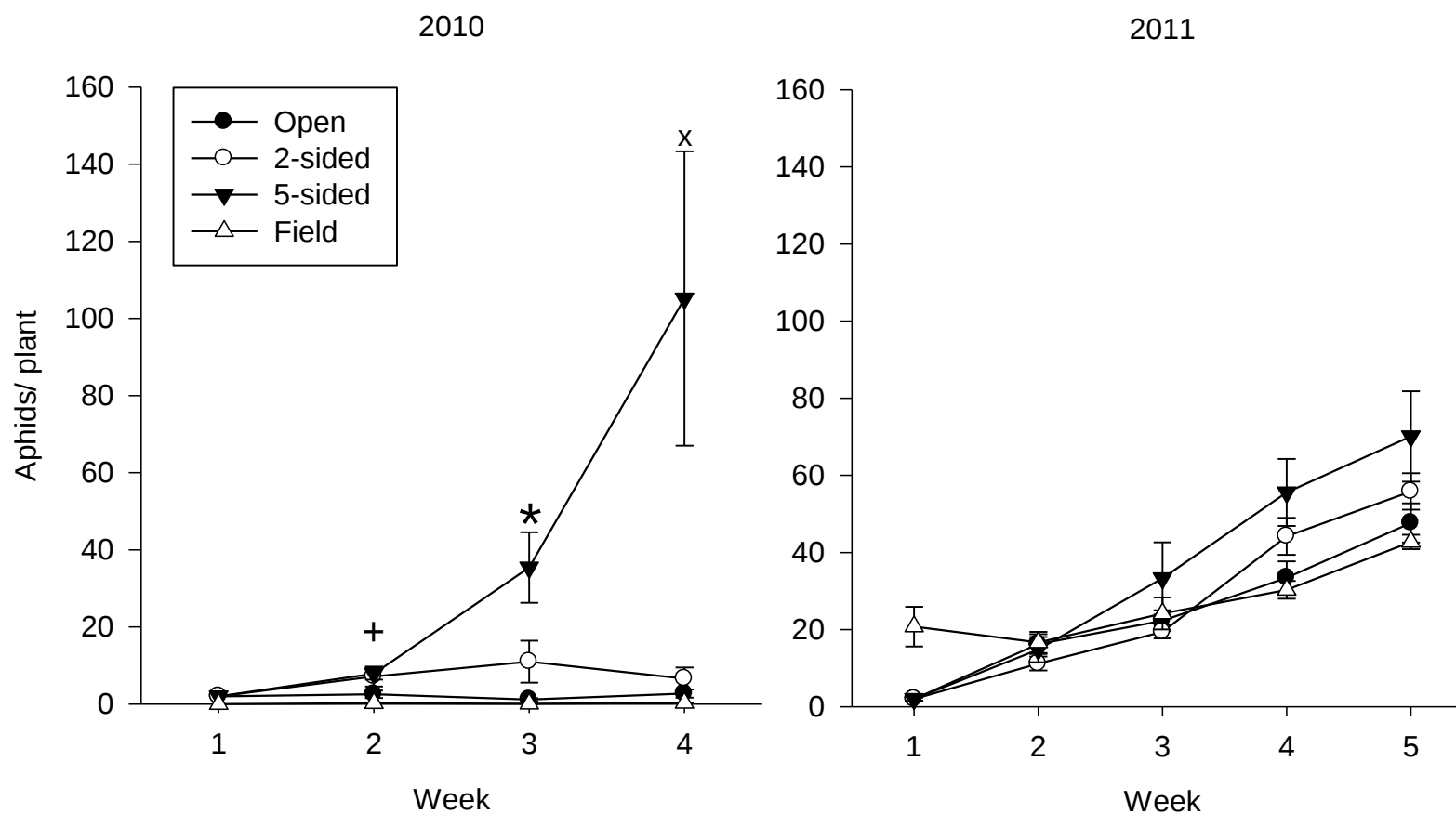


Figure 3.3: Mean number of *A. glycines* observed per plant each week in soybean fields outside of plots and in open, 2- and 5-sided treatment plots in 2010 and 2011. Symbols indicate significantly more aphids in (+) 5-sided and 2-sided than in open plots, (*) between all treatments and (x) in 5-sided than in open or 2-sided plots.



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CHAPTER IV: Diel variation in natural enemy communities of *Aphis glycine* in soybean.

Abstract

Nocturnally-active predators can make important contributions to insect pest suppression in agroecosystems. In particular, nocturnal predators have been shown to be responsible for significant predation of herbivores within soybean fields. In spite of this fact, much of the existing research on *A. glycines* natural enemies has focused on members of the diurnal predator community. Here, we assess diel variation of the predator community and *A. glycines* predation events in soybean with vacuum samples, direct observations, and video observations. The majority of predation events observed (95%) occurred during daylight hours and primarily by anthocorids (81%), followed by chrysopid larvae (10%), and one each by a coccinellid, and a predatory mite. The sole nocturnal predation event observed was a by a spider. We found that anthocorids and nabids were most active in the afternoons and carabids were more active at night. Spiders and anthocorids were the most abundant predatory arthropods captured in vacuum samples. In contrast, on video samples, lacewing larvae were most active during the day and lacewing larvae, spiders, opiliones and carabids were similarly active at night. The differences between the two sample methods suggests that vacuum samples may represent predator abundance more accurately, while video data can be used to better assess relative time spent foraging.

Introduction

The soybean aphid, *Aphis glycines*, is an invasive insect pest from China with the potential to cause significant yield losses in soybean (Difonzo and Hines 2002). Since *A. glycines* was first discovered in the U.S. in 2000, it has been the subject of much study (Ragsdale et al.

2011). A number of studies have focused on identifying the natural enemies that attack *A. glycines* (Rutledge et al. 2004, Allard and Yeargan 2005, Mignault et al. 2006, Hajek et al. 2007, Kaiser et al. 2007, Pike et al. 2007, Hannam et al. 2008, Noma and Brewer 2008) and their relative efficacy (Fox et al. 2005, Desneux et al. 2006, Costamagna and Landis 2007). However, most of these studies have focused on the diurnal predator community within soybean fields. For example, Costamagna and Landis (2007), conducted direct observations of soybean aphid predation within soybean fields, between 10:00 and 21:00 h.

In contrast, little work has examined the effect of nocturnal natural enemies on soybean aphid populations, despite the fact that these taxa have been demonstrated to make important contributions to pest suppression in soybean fields. Nocturnally-active nabids were the most abundant predator and were responsible for up to half of *Helicoverpa zea* egg predation observed in soybean fields in Kentucky (Pfannenstiel and Yeargan 2002). Similarly, nocturnal spiders were responsible for 98% of lepidopteran egg predation in soybean fields in Texas (Pfannenstiel 2008). Nocturnally-active spiders have been observed at similar abundances and foraging at similar frequencies as diurnally-active coccinellid beetles in Michigan soybean fields (L. Petersen and J.M. Woltz unpub. data). Spiders can be effective natural enemies and an important component of the natural enemy guild (Riechert and Lockley 1984, Sunderland 1999) and are capable of suppressing aphid populations (Gavish-Regev et al. 2009). Additionally, spiders can cause trophic cascades. Higher spider density can lead to more pest consumption and lower leaf damage in soybean (Carter and Rypstra 1995, Rypstra and Carter 1995).

Multiple sampling methods are available for assessing natural enemy communities. The efficacy of different methods varies with the vagility and mode of dispersal of taxa sampled (Schmidt et al. 2008). Additionally, various trade-offs exist between spatial and temporal

coverage of sampling methods and the type of information each can generate. Traditional sampling methods such as pitfall traps, sweep netting, and sticky traps can be employed repeatedly over large areas and can provide information about natural enemy community composition, but provide no information about the relative efficacy of various taxa. Direct human observation can elucidate specific interactions, but is typically limited in the length and number of observations possible. In contrast to these temporal limitations, video observations can be made continuously, although over limited spatial areas (Grieshop et al. 2012).

Given the potential for significant soybean aphid suppression from the nocturnal community, our objectives were to: 1) assess diel variation in the predator community in soybean; 2) contrast rates of soybean aphid predation during night and day. Additionally, our third objective was to 3) compare the predator communities described by vacuum sampling, direct observations, and video observations.

Methods: Direct observation study

Study locations. This study was conducted between 6 June and 13 July 2012 in three conventionally-managed soybean fields in southern Michigan (Table 4.1). The study was conducted early in the growing season (soybean plants between growth stages of V1-V5) because early season dynamics are important for preventing outbreaks (Rutledge et al. 2004). No fields planted with systemic insecticide-treated seed were used in this study. Agriculture in this region consists primarily of annual field crops (corn, soy, wheat) and perennial forage crops (pasture, alfalfa), while non-crop areas are primarily deciduous forest. Three separate 24 h predation studies were conducted in each field for a total of n=9 surveys.

Plot establishment. In each field, four 10 x 10 m plots were established for soybean aphid predation surveys (Figure 4.1). Each plot encompassed 14 rows of soybean planted on a

row spacing of 76.2 cm. Two “edge” plots were situated between 0 and 10 m into the field, while two “interior” plots were situated between 50 and 60 m into the field. The plots were at least 50 m from other field edges in all other directions.

Aphid infestation. *Aphis glycines* used in this study were reared under conditions of predator exclusion in Lumite field cages (Lumite Inc, Baldwin, GA) in soybean fields at the Michigan State University Department of Entomology Research Farm. Soybean leaves containing aphids were removed from rearing cages and transferred to experimental fields in coolers.

Within each plot, ten plants were randomly selected for aphid infestation (Figure 4.1). First, ten numbers between one and fourteen were randomly generated without duplication to select rows within plots. Then, ten numbers between one and ten were randomly selected to determine the position in meters of the plant within the row. Ten aphids of mixed age classes were transferred to the selected plants using a fine-haired paint brush. Aphids were placed in clip cages on the underside of the upper most fully-opened leaf and allowed to settle for at least 1 h before cages were removed. Plants were searched for naturally-occurring soybean aphids at infestation, and any found were removed.

During each monitoring period, one interior and one edge plot were infested between 18:00 and 20:00 h. Clip cages were removed at dusk (approx. 21:00-22:00 for each of our surveys) to begin nocturnal surveys. The other interior and edge plots were infested between 3:00 and 5:00, and clip cages were removed at sunrise (approx. 6:00 for each of our surveys) to begin diurnal surveys.

Additionally, ten “caged” plants from which predators were excluded were used to account for aphid mortality not due to predation. Five predator exclusion cages were located

between the two interior plots and five between the two edge plots (Figure 4.1). Exclusion cages consisted of two 50 cm flexible metal rods bent over the plant in crossed arches to create a frame. A 19 L paint strainer bag was placed around the frame and buried in the soil to a depth of 5 cm. The tip of the bag was cut to allow aphid counts and tightly retied with a twist-tie in between surveys. Five caged plants were infested prior to dusk and five additional plants were infested prior to dawn, at the same time as the interior and edge plots.

Aphid surveys. The number of aphids on each plant was counted at clip cage removal to account for reproduction or mortality that might have occurred within the clip cages. Aphids on plants infested before dusk were counted every 3 h for 24 h at 21:00, 0:00, 3:00, 6:00, 9:00, 12:00, 15:00, 18:00, and 21:00. Aphids on plants infested before dawn were counted on each plant at 6:00, 9:00, 12:00, 15:00, 18:00, and 21:00. With three replicate surveys within three fields and two sampling locations (edge and interior) and two infestation periods (pre-dusk and pre-dawn) and ten plants within each plot, 360 plants were surveyed at each time period ($3 \times 3 \times 2 \times 2 \times 10 = 360$), with the exception of the 0:00 and 3:00 time periods which were not replicated in pre-dawn infested plots ($3 \times 3 \times 2 \times 10 = 180$). The 6:00 samples approximately coincided with dawn and the 21:00 samples coincided with dusk. At night, aphids were counted using Petzl Tactikka Plus LED headlamps with red filters to minimize disturbance of nocturnally-active insects.

Predator sampling. During the predation surveys, prior to counting aphids, plants were visually inspected and any predatory insects or arachnids observed on the infested leaves were recorded as well as whether or not they were observed feeding on *A. glycines*. Additionally, predators were sampled on foliage three times/ d using a leaf blower (BG 56 C-E; Stihl, Waiblingen, Germany) used in reverse as a vacuum to suck insects off of plants and into fine

mesh collection bags. At 10:00, 16:00, and 22:00, field workers walked along five 20 m transects outside of the survey plots with the vacuum tube placed at the tops of the soybean plants. Insects sucked into the tube were captured in 1-gallon mesh paint strainer bags placed inside the mouth of the tube and secured with rubber bands. Transects outside of the edge plots ran from 0-20 m into the field. Transects outside of interior plots ranged from 40-60 m into the field. Each transect was at least 50 m from the plot to avoid removing predators that might have otherwise migrated into the plots during subsequent sampling periods, and different transects were used after each sampling period. A single mesh bag was used for all five transects during a sampling period, unless excess leaf debris reduced suction. When multiple bags were used, samples were combined prior to sorting. After each collection, the mesh bags were secured with rubber bands and placed into a 18.9 L bucket with a lid, containing plaster of Paris soaked in ethyl acetate to kill the insects. Insects and arachnids were identified to family or order in the laboratory. Voucher specimens were deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University (Table 4.2).

Temperature. A thermometer (Extech 445713, Extech Instruments, Nashua, NH) was placed at soybean canopy height in the center of each plot to record temperature. Readings were taken after each predation survey was completed, so as not to disturb predator feeding.

Statistical analysis. *Aphid surveys:* The change in aphids over each 3 h time period was analyzed using a general linear mixed model (PROC GLIMMIX; SAS 9.2, SAS Institute, Cary, NC). Plant location (Interior, Exterior, or Caged) and time period were fixed effects and site X survey was treated as a random block. Change in aphid numbers was not treated as repeated measures. Direct population counts are typically treated as repeated measures because the population in one time period is dependent upon the population in the previous time period. In

contrast, the change in aphid numbers during one time period is not expected to be dependent upon the change in the previous one. Additionally, a plot of the model residuals by time period showed no patterns, indicating that repeated measures were unnecessary to account for temporal autocorrelation.

Vacuum samples: Analysis of Similarity (ANOSIM, PRIMER 6.0) was used to describe differences in the predator community by time of day (morning, afternoon, evening) and site. Preliminary analyses indicated no community differences between edge and interior samples. First, a Bray-Curtis Similarity Index was calculated for each pair of samples, indicating the degree of similarity in community composition between the samples. A value of zero indicates complete dissimilarity (no common species) and a value of 100 represents completely similar samples (both samples have the same species in the exact same abundances). The similarity between a given sample and every other sample is ranked, and this is repeated for each sample. ANOSIM is conducted on the rank similarities, with the null hypothesis that site and time of day have no effect on the rank similarities between samples. An R statistic is calculated (analogous to an F statistic in ANOVA). The significance of the R statistic is calculated by randomly reassigning samples to different sites and times of day and recalculating the R statistic. This is repeated 999 times, and the number of times that an R statistic greater than or equal to the one calculated for the actual data is achieved by chance is divided by the number of permutations to achieve a significance level.

Methods: Video observation study

Study location. This experiment was conducted in a 1 ha soybean field on the Michigan State University Department of Crop and Soil Sciences Research Farm (Table 4.1). Eight soybean plants within the field were selected for around-the-clock monitoring of aphid colonies and predation events from 22 to 29 June 2012.

Aphids surveys. The uppermost trifoliolate of each focal soybean plant was infested with ten soybean aphids of mixed age class at the beginning of the experiment. After infestation, aphids were enclosed in a clip cage for 1 h to allow them time to settle and begin feeding. Clip cages consisted of a 1 cm section of 1.8 cm PVC pipe. One opening of the pipe was covered in fine-mesh brass screen to allow air exchange. The other was enclosed with a 1 cm² plastic microscope slide. The two coverings were attached to the PVC with a metal hair barrett, allowing the cage to be attached to plant leaves. The number of aphids on each soybean plant was counted every 3 h for 7 d at 0:00, 3:00, 6:00, 9:00, 12:00, 15:00, 18:00, and 21:00 h.

Video observations. Digital surveillance equipment was used to record predators foraging on soybean plants 24 hr /d, adapting the methods of Greishop et al. (2012). Eight water-proof outdoor video surveillance cameras (QOCD36, Q-See.com, Anaheim, CA) were deployed in a soybean field. The cameras were distributed in a semi-circle around the central digital video recorded (DVR; Figure 4.2). Cameras were suspended 10 cm above the tops of focal soybean plants from PVC frames placed perpendicular to soybean rows and anchored with rebar (Figure 4.2). The cameras were connected by coaxial cables to a multi-channel H.264 Network DVR (Security Hardware Store, LLC, Boise, ID), where video was recorded onto a 500GB Seagate SV35.5 internal hard drive. The cameras and DVR were powered by a pair of Die Hard RV/ marine batteries linked in series. The DVR and batteries were housed in a 75.7 L

plastic storage tub with lid to keep the equipment dry. Holes were cut in the sides of the tub to feed power and coaxial cables through and to allow for ventilation to prevent the DVR from over-heating.

Cameras were moved up the frames as needed to maintain ten cm height above soybean canopy. Cameras were pointed at the uppermost trifoliate, and adjusted twice daily to account for changes in the plant's position. Video could be viewed as it was being recorded on a 18 cm digital LCD TV (Haier) connected to the output channel of the DVR. This allowed us to confirm that we were recording the desired part of the plant.

Video processing. After 7 d of recording, the video files were transferred from the hard drive in the DVR to an external hard drive (Fantom GreenDrive, MicroNet, Torrance, CA) and converted to AVI files for viewing. Lab workers watched four videos at a time at 4x speed, to identify frames with insect activity, after which, insect activity was viewed one video at a time at 1x speed. The taxonomic identity (family or order), arrival time, behavior, and departure time of each insect was recorded. Arthropods of the same taxonomic group that left and re-entered the screen within five minutes were considered a single individual. An arthropod of the same taxonomic group that re-entered the screen after a period of greater than five minutes was recorded as a separate individual.

Statistical analysis. *Aphid surveys:* The change in aphids over each 3 h time period was compared using a general linear mixed model (PROC GLIMMIX; SAS 9.2, SAS Institute, Cary, NC). Time period was treated as a fixed effect and day was used as a random block. As in the direct observation study, change in aphid numbers was not treated as repeated measures and a plot of the model residuals by time period showed no evidence of temporal autocorrelation.

Vacuum samples: ANOSIM (PRIMER 6.0) was used as described above to examine differences in the predator community by time of day (morning, afternoon, evening).

Video data: ANOSIM (PRIMER 6.0) was also used to examine differences in the predator community observed on the video at night (predators viewed between 21:00 and 6:00) and day (predators viewed between 6:00 and 21:00).

Results: Direct observation study

Colony establishment. Establishment success varied among infestation periods (Figure 4.3). Establishment was more successful in the evening versus pre-dawn infestation, but in both cases was similar between caged and uncaged plants, suggesting that initial establishment success or failure was not directly related to predation. Six hours after pre-dusk infestation, aphid populations on both caged and uncaged plants decreased in 32.5% and 35.6% of cases, remained the same in 22.5% and 28.3% of cases, and increased in 45% and 35.6% of cases. However, for pre-dawn infested plants, initial mortality was much greater. Aphid populations on caged and uncaged plants decreased in 67.5% and 68.3% of cases, remained the same in 20% and 15%, and increased in only 12.5% and 16.7% of cases.

Aphid surveys. On average, during the first 24 h after infestation, aphids either decreased or changes were not significantly different from zero in all time periods. There was no effect of location within field on change in aphid numbers ($F_{2,15}=1.22$, $p=0.32$), suggesting that aphid population changes did not differ between exterior and interior plots. Additionally, population changes did not differ between caged and uncaged plants. There were marginal differences in aphid decreases between time periods ($F_{2,56}=1.97$, $p=0.08$). There were marginally larger aphid decreases from 6:00-9:00 than from 18:00-21:00 and 21:00-0:00, and significantly higher aphid decreases from 6:00-9:00 than from 3:00-6:00, 12:00-15:00, and

15:00-18:00 (Table 4.3). There were significant time period X location interactions ($F_{14,105}=2.01$, $p=0.02$); however, there were no consistencies for location effects across time periods.

Temperature. Temperatures ranged from 11.8 to 41.3 °C. Recorded temperatures were within physiological tolerance limits of *A. glycines* (McCornack et al. 2004, McCornack et al. 2005) except for the periods from 12:00-15:00 and 15:00-18:00 in the second and third surveys in Westphalia and all three surveys in Mason. Temperatures during these periods exceeded 35 °C. However, given that aphid decreases during the time periods 12:00-15:00 and 15:00-18:00 were actually significantly lower than from 6:00-9:00, it is unlikely that high temperatures explain aphid mortality. Additionally, removing data points from times in which temperatures exceeded 35 °C did not alter statistical outcomes.

Predator observations. Predators were observed infrequently during our direct observations. During 2,520 observations, we directly observed 68 predators foraging on our infested soybean plants during aphid surveys. Anthocorid nymphs and adults were the most abundant predator observed ($n=44$ individuals), followed by spider adults and immatures (8 individuals) and coccinellid adults (6 individuals; Table 4.4). With the exception of anthocorids, which were most frequently observed in the afternoon hours, other predators were not observed at sufficient frequency to ascertain diel patterns.

Additionally, we directly observed 22 predation events on soybean aphid. Of these events, seventeen were by anthocorids, two by chrysopid larvae, one by a coccinellid, one by a spider and one by a predatory mite. All directly observed predation events occurred during the daylight hours, except for one predation event by a spider which occurred at 0:00 hours.

Vacuum samples. Spiders and anthocorids were the most abundant predatory arthropods captured in vacuum samples. In 49 vacuum samples, we collected 780 anthocorids and 371 spiders. Eight coccinellids were collected. The predator community sampled differed significantly between all sites ($R=0.492$, $p=0.001$) and by time of day ($R=0.182$, $p=0.002$). Predator communities were not different in the morning (10:00) and afternoon (16:00) samples ($R=0.080$, $p=0.16$), but were significantly different between night samples (22:00) and morning or afternoon samples ($R=0.173$, $p=0.02$; $R=0.297$, $p=0.003$, respectively). In general, more anthocorids and nabids were collected in the afternoon (Table 4.5). Elaterids were found only at night, and coccinellids and staphylinids were found only during the day (Table 4.6).

Results: Video observation study

Aphid surveys. There was a significant effect of time on the amount of change in aphid numbers ($F_{7,39}=5.24$, $p=0.0003$). Aphids increased by an average of 7.29 ± 1.37 individuals/plant between 6:00 and 9:00, while aphid changes during all other time periods were not significantly different from zero (Table 4.7).

Temperature. Temperatures ranged from 7.9 to 40.85 °C. Recorded temperatures were within physiological tolerance limits of *A. glycines* (McCornack et al. 2004, Mccornack et al. 2005) except for the periods from 12:00-15:00 and 15:00-18:00 on 26-28 June and 9:00-12:00 on 28 June. Temperatures during these periods exceeded 35 °C. However, removing data points from times in which temperatures exceeded 35 °C did not alter statistical outcomes.

Vacuum samples. Spiders and anthocorids were the most abundant predatory arthropods captured in vacuum samples (Table 4.8). In 18 vacuum samples we collected 143 anthocorids and 247 spiders. Six coccinellids were captured. The predator community differed significantly by time of day ($R=0.206$, $p=0.025$). Predator communities were not different in the morning

(9:00) and afternoon (15:00) samples ($R=0.181$, $p=0.12$), but were significantly different between night (0:00) and morning or afternoon ($R=0.259$, $p=0.073$; $R=0.206$, $p=0.031$, respectively). In general, there were more anthocorids and nabids in the afternoon (Table 4.5) and coccinellids were only found during the day (Table 4.8). Unlike the vacuum samples from the direct observation study, no elaterids, staphylinids, or lampyrids were captured (Table 4.8).

Video data. Due to intermittent technical difficulties with our video recording equipment, we were not able to record continuously during the observation period. However, we have three to six replicate days of video data following eight plants for each 3 h time period (Tables 4.9, 4.10), providing a total of 792 hours of video watched. Chrysopid larvae were the most common predator observed ($n=41$), followed by spiders ($n=22$), carabids ($n=29$), and coccinellids ($n=8$). Additionally, 35 coleopterans that could not be identified to family level were observed. The predator community observed on video did not differ between time periods ($R=0.032$, $p=0.31$), or broadly between night and day ($R=0.029$, $p=0.29$), although there were more carabids observed during the night (Table 4.5). However, the data showed similar patterns to that of Petersen and Woltz (in prep.), with opiliones only present at night, and coccinellids only present during the day (Tables 4.9, 4.10). Ants and lacewing larvae were the most abundant predators observed during the day. Ants, carabids, spiders, opiliones, and lacewing larvae were the most abundant predators observed at night.

Discussion

Aphid colony establishment. Given the demonstrated importance of nocturnal predators on other pests in soybean (Pfannenstiel and Yeargan 2002, Pfannenstiel 2008), we expected to observe significant soybean aphid reduction during night hours. Instead, most directly observed predation events occurred during daylight hours. Unfortunately, the nature of our directly

observed aphid data prevents us from attributing aphid population changes to predation. Specifically, the lack of difference between aphid population patterns on caged and open plants in the direct observation study suggests that aphid population declines in this study were not solely the result of predation events. While we have successfully transferred aphids for experiments many times in the past (Fox et al. 2004, 2005, Costamagna and Landis 2006, Costamagna et al. 2007, Costamagna et al. 2008, Gardiner et al. 2009, Woltz et al. 2012, Woltz and Landis 2013), we have typically followed the resulting aphid populations over weekly periods. As such, we have rarely monitored establishment success rate in the short-term. In one instance in which aphid populations were monitored within 24 h of infestation, there was approximately 25% mortality in exclusion cages from which aphids could not emigrate and to which predators had no access (Fox 2002). The average 24 h declines in adult aphids on our pre-dusk infested plants was about 40-45% regardless of cage status, indicating high initial mortality. We suspect that the demands of our study, i.e. transferring large numbers of aphids in a short time period, may have led to this increased mortality and masked any potential predator effects in the 24 h observation period. In contrast, the video study, which was conducted over 7 d, revealed a diel pattern in aphid population change with aphids increasing in the early daylight hours and declining or remaining steady thereafter.

Predator sampling method comparison. Our study does allow us to assess diel patterns in soybean predator communities and to compare methods of predator sampling. Video data suggest that carabids are more active at night. Vacuum samples and direct observations suggest that anthocorids are more active in the afternoons. Additionally, vacuum samples from the two different studies showed similar statistical patterns and trends for several taxa. In both, spiders and anthocorids were the most abundant predatory taxa collected. Similarly, in both, coccinellids

were only captured during the day, and anthocorids and nabids were more abundant in afternoon samples. The major differences, including the absence of some taxa and differences in diel patterns of others, could reflect differences in the broader predator community over space (i.e. the samples were collected from sites spread across lower Michigan) or time (the samples were collected during different periods of the summer growing season). Additionally, differences occurring at the species level could influence overall diel patterns.

In contrast to the vacuum samples, spiders and anthocorids were not the most abundant predatory arthropods observed on the video. Instead, ants and chrysopid larvae were the most abundant taxa observed during the day and ants, chrysopid larvae, carabids, spiders and opiliones were observed most frequently at night. These differences could be due to multiple factors. In the case of anthocoridae, these tiny insects (1-5 mm) move relatively slowly and are very difficult to identify on video. Therefore, they were likely not recorded in exact proportion to their actual abundance. For the other, larger, easier to identify taxa, the differences could reflect differences in relative abundance versus time spent foraging. Chrysopid larvae may have had lower overall abundances within the field, but would be captured more frequently on video if they spent more time foraging than more abundant taxa. While this may not reflect their true abundances as well as a vacuum sample, this type of foraging-activity data may be more relevant for biological control since it could better reflect the likelihood that a natural enemy will encounter a prey item.

Regardless of the sampling methods used, the relative efficacy of predatory taxa must be considered when assessing the predator community. Single, particularly effective natural enemy species can be responsible for the majority of pest suppression in simplified agricultural systems (Hawkins et al. 1999, Straub and Snyder 2006, Frank et al. 2007). Therefore, without estimates of the relative efficacy of different predators, observation methods assessing the numbers of

predators on plants could underestimate the importance of highly mobile predators to soybean aphid suppression (Schmidt et al. 2008). For example, infrequent visits by mobile predators may be sufficient to suppress soybean aphid populations in years with low aphid pressure (Woltz and Landis 2013).

Coccinellids were sampled infrequently relative to resident predators like spiders and anthocorids. The low coccinellid activity-density is not surprising given that aphid densities within fields were low (Woltz pers. obs.). While at high aphid densities coccinellids will begin to aggregate and to initiate oviposition, at low aphid densities coccinellids disperse through soybean fields consuming aphids they encounter. This predation from infrequently occurring coccinellids, combined with predation from resident predators, is thought to be sufficient to suppress insipient aphid colonies and prevent them from contributing to outbreaks at the field-level (Costamagna and Landis 2011). Anthocorids, in contrast, were abundant by most sampling measures. Anthocorids are present in soybean fields throughout the growing season and consume a variety of soybean herbivores, with the result that anthocorid abundances within soybean fields are less closely linked to soybean aphid density than those of coccinellids (Rutledge et al. 2004). In fact, the ability of anthocorids to be present in soybean fields prior to soybean aphid arrival allows them to help prevent early-season aphid population increases (Rutledge et al. 2004, Rutledge and O'Neil 2005).

Use of video data in natural enemy surveys. For the aphid populations followed in the video study, there are no paired caged plants to assess how well the populations were established. Ideally, the video data should allow us to match up population changes on individual plants with predators foraging on those plants during that period of time. However, due to technical difficulties, video was not available for every period of time on every plant. For the

video that is available, large population decreases in aphids occur during some 3 h blocks in which no predators were recorded. This does not mean that no predators were present on the plant at those times. In some cases, arthropods were observed but were not recorded because identification even to order was impossible. In other cases, aphids dispersed from the focal point of the camera to other parts of the plant. In these cases, predation could have happened off-screen. Given these limitations, I conclude that video surveillance has limited usefulness for recording predation of mobile prey on moving plants. In contrast, others (Merfield et al. 2004, Frank et al. 2007, Grieshop et al. 2012) have had excellent success recording predation events of immobilized prey on non-moving surfaces such as Petri dishes or tree limbs. Despite our difficulties in observing aphid predation, video surveillance remains useful as a tool to survey the predator community, even in a habitat with moving focal plants. Video data can give more detailed information about frequency of foraging on plants, in comparison with more traditional sampling methods (e.g. pitfall traps, sticky traps, vacuum sampling), which can indicate relative abundance but do not necessarily provide information about time spent on plants. We found differences in the relative abundances of predators indicated by the vacuum samples and their relative foraging frequencies as observed on video. Similar differences have been found for ground-foraging predators. In a study in which carabids and chilopodans represented the majority of captures in pitfall traps, these taxa were infrequently recorded consuming sentinel prey (Grieshop et al. 2012). Additionally, video may provide better evidence of true diel activity patterns as vacuum samples may capture inactive individuals that remain in the habitat during their inactive period.

APPENDIX

Chapter IV Tables and Figures

Table 4.1: Field locations and characteristics for direct and video observation of *A. glycines* predator communities and predation events.

Study	Location	Coordinates		Size (ha)	Survey dates	Vegetative stage
Direct observation	Frankenmuth, MI	43 24' 37.77" N	83 42' 06.90" W	30	6-12 June	V1-V2
	Westphalia, MI	42 51' 57.77" N	84 48' 04.87" W	14	16-20 June	V1-V2
	Mason, MI	42 37' 38.58" N	84 25' 50.15" W	32	10-13 July	V5
Video observation	East Lansing, MI	42 42' 51.86" N	84 27' 52.31" W	1	22-29 June	V3

Table 4.2: Record of deposition of voucher specimens for Chapter IV. The specimens listed below have been deposited in the Albert J. Cook Arthropod Research Collection, Michigan State University (MSU) museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number 2013-08 have been attached or included in fluid preserved specimens.

Order	Family	Life Stage	Quantity	Preservation
Coleoptera	Lampyridae	Adult	3	Pinned
Coleoptera	Elateridae	Adult	3	Pinned
Coleoptera	Carabidae	Adult	3	Pinned
Coleoptera	Staphylinid	Adult	3	Pinned
Hemiptera	Nabidae	Adult	3	Pinned
Hemiptera	Anthocoridae	Adult	3	Pinned
Neuroptera		Larvae	5	70% EtOH
Opiliones		Adult/nymph	5	70% EtOH
Araneae		Adult/nymph	5	70% EtOH

Table 4.3: Means $\pm$ S.E. of aphid change during each time period of the direct observation study. Bold indicates means that were significantly different from zero. Different letters indicate means which are significantly different from one another.

Time period	Mean aphid change $\pm$ SE	
6:00-9:00	-1.16 $\pm$ 0.26	A
9:00-12:00	-0.67 $\pm$ 0.26	AB
0:00-3:00	-0.52 $\pm$ 0.28	AB
18:00-21:00	-0.51 $\pm$ 0.26	AB
21:00-0:00	-0.43 $\pm$ 0.28	AB
15:00-18:00	-0.32 $\pm$ 0.26	B
3:00-6:00	-0.23 $\pm$ 0.28	B
12:00-15:00	0.10 $\pm$ 0.26	B

Table 4.4: Predators directly observed during 24 h aphid surveys. Observations were made 180 times at 0:00 and 3:00 h, and 360 times at all other time periods.

	6:00	9:00	12:00	15:00	18:00	Day total	21:00	0:00	3:00	Night total
Araneae	1	0	1	1	0	3	0	4	1	5
Opiliones	1	0	0	0	0	1	0	0	0	0
Cantharid	0	1	0	0	0	1	0	0	1	1
Carabidae	2	0	0	0	0	2	0	0	1	1
Coccinellid	0	1	1	0	2	4	0	1	1	2
Lampyrid	1	0	0	0	0	1	0	0	0	0
Anthocoridae	5	5	9	11	7	37	1	3	3	7
Chrysopidae larva	0	0	0	0	2	2	0	0	0	0
Syrphidae larva	1	0	0	0	0	1	0	0	0	0

Table 4.5: Diel comparisons in predatory taxa from vacuum and video samples.

Study	Taxon	Diel comparison	
Vacuum samples, direct observation study	anthocoridae	afternoon > morning	$t_{46}=2.09, p=0.04$
		afternoon > night	$t_{46}=2.32, p=0.02$
	nabidae	afternoon > night	$t_{46}=2.08, p=0.04$
Vacuum samples, video observation study	anthocoridae	afternoon > morning	$t_{15}=1.88, p=0.08$
		afternoon > night	$t_{15}=2.48, p=0.03$
	nabidae	afternoon > morning	$t_{15}=1.89, p=0.08$
		afternoon > night	$t_{15}=2.42, p=0.03$
Video samples	carabidae	night > day	$t_{262}=3.00, p=0.003$

Table 4.6: Mean $\pm$ S.E. number of predator individuals collected in vacuum samples of the direct observation study at morning (10:00), afternoon (16:00), and night (22:00).

	Sample times		
	Morning	Afternoon	Night
Araneae	6.73 $\pm$ 2.72	7.06 $\pm$ 1.50	8.94 $\pm$ 1.47
Opiliones	1.33 $\pm$ 0.60	2.61 $\pm$ 1.14	1.44 $\pm$ 0.68
Carabidae	0.07 $\pm$ 0.07	0.33 $\pm$ 0.23	0 $\pm$ 0
Coccinellidae	0.33 $\pm$ 0.16	0.17 $\pm$ 0.12	0 $\pm$ 0
Elateridae	0 $\pm$ 0	0 $\pm$ 0	0.69 $\pm$ 0.20
Lampyridae	0.13 $\pm$ 0.09	0.06 $\pm$ 0.06	0.25 $\pm$ 0.25
Staphylinidae	0.60 $\pm$ 0.40	0.28 $\pm$ 0.13	0 $\pm$ 0
Anthocoridae	11.4 $\pm$ 2.96	24.78 $\pm$ 5.53	10.19 $\pm$ 2.30
Nabidae	0.40 $\pm$ 0.16	1.72 $\pm$ 0.88	0.38 $\pm$ 0.26
Chrysopidae larvae	0.47 $\pm$ 0.34	0.67 $\pm$ 0.27	0.69 $\pm$ 0.36

Table 4.7: Mean $\pm$ S.E. of aphid colony size change during each time period of the video observation study. Means shown in bold are significantly different from zero. Different letters indicate means which are significantly different from one another.

Time period	Mean aphid change $\pm$ SE	
6:00-9:00	7.29 $\pm$ 1.37	A
9:00-12:00	0.52 $\pm$ 1.37	B
18:00-21:00	0.09 $\pm$ 1.37	B
3:00-6:00	-1.17 $\pm$ 1.48	B
21:00-0:00	-1.3 $\pm$ 1.37	B
12:00-15:00	-1.52 $\pm$ 1.37	B
15:00-18:00	-2.05 $\pm$ 1.37	B
0:00-3:00	-2.67 $\pm$ 1.48	B

Table 4.8: Mean $\pm$ S.E. number of predator individuals collected in vacuum samples during the video observation study at morning (9:00), afternoon (15:00) and night (0:00).

	Sample times		
	Morning	Afternoon	Night
Araneae	24.75 $\pm$ 2.02	13.57 $\pm$ 5.19	7.57 $\pm$ 1.62
Opiliones	0.25 $\pm$ 0.25	0.43 $\pm$ 0.30	0.14 $\pm$ 0.14
Carabidae	0 $\pm$ 0	0.14 $\pm$ 0.14	0.57 $\pm$ 0.43
Coccinellidae	0.5 $\pm$ 0.29	0.57 $\pm$ 0.43	0 $\pm$ 0
Elateridae	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Lampyridae	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Staphylinidae	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Anthocoridae	4.75 $\pm$ 3.47	14.71 $\pm$ 5.65	3.00 $\pm$ 1.38
Nabidae	1.00 $\pm$ 0.71	8.71 $\pm$ 3.52	0.71 $\pm$ 0.42
Chrysopidae larvae	0.75 $\pm$ 0.75	0.14 $\pm$ 0.14	1.00 $\pm$ 1.00

Table 4.9: Mean $\pm$ S.E. number of predator individuals observed in daylight hours during each three hour period of video surveillance.

	6-9	9-12	12-15	15-18	18-21	Day total
# days video	3	3	4	6	5	
Aranae	0 $\pm$ 0	0.21 $\pm$ 0.10	0.13 $\pm$ 0.13	0.04 $\pm$ 0.03	0.03 $\pm$ 0.03	0.07 $\pm$ 0.03
Opiliones	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Carabidae	0.08 $\pm$ 0.06	0.08 $\pm$ 0.06	0.06 $\pm$ 0.04	0 $\pm$ 0	0.05 $\pm$ 0.03	0.05 $\pm$ 0.02
Coccinellidae	0 $\pm$ 0	0.21 $\pm$ 0.10	0 $\pm$ 0	0.02 $\pm$ 0.02	0.05 $\pm$ 0.03	0.05 $\pm$ 0.02
Coccinellidae larvae	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0.03 $\pm$ 0.03	0.01 $\pm$ 0.01
Lampyridae	0.04 $\pm$ 0.04	0 $\pm$ 0	0.06 $\pm$ 0.04	0.04 $\pm$ 0.03	0 $\pm$ 0	0.03 $\pm$ 0.01
Anthocoridae	0.04 $\pm$ 0.04	0 $\pm$ 0	0 $\pm$ 0	0.06 $\pm$ 0.04	0.15 $\pm$ 0.09	0.06 $\pm$ 0.02
Nabidae	0 $\pm$ 0	0.08 $\pm$ 0.06	0 $\pm$ 0	0.02 $\pm$ 0.02	0 $\pm$ 0	0.02 $\pm$ 0.01
Chrysopidae	0 $\pm$ 0	0.04 $\pm$ 0.04	0 $\pm$ 0	0 $\pm$ 0	0.03 $\pm$ 0.03	0.01 $\pm$ 0.01
Chrysopidae larvae	0.04 $\pm$ 0.04	0.38 $\pm$ 0.19	0.13 $\pm$ 0.07	0.13 $\pm$ 0.06	0.25 $\pm$ 0.10	0.18 $\pm$ 0.04

Table 4.10: Mean $\pm$ S.E. number of predator individuals observed in night hours during each three hour period of video surveillance.

	21-0	0-3	3-6	Night total
# days video	5	4	3	
Araneae	0.10 $\pm$ 0.05	0.06 $\pm$ 0.04	0.17 $\pm$ 0.10	0.10 $\pm$ 0.03
Opiliones	0 $\pm$ 0	0.19 $\pm$ 0.08	0.21 $\pm$ 0.10	0.11 $\pm$ 0.04
Carabidae	0.20 $\pm$ 0.13	0.31 $\pm$ 0.13	0.13 $\pm$ 0.07	0.22 $\pm$ 0.07
Coccinellidae	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Coccinellidae larvae	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Lampyridae	0.03 $\pm$ 0.03	0 $\pm$ 0	0 $\pm$ 0	0.01 $\pm$ 0.01
Anthocoridae	0 $\pm$ 0	0 $\pm$ 0	0.04 $\pm$ 0.04	0.01 $\pm$ 0.01
Nabidae	0.10 $\pm$ 0.05	0.03 $\pm$ 0.03	0 $\pm$ 0	0.05 $\pm$ 0.02
Chrysopidae	0.05 $\pm$ 0.03	0 $\pm$ 0	0.04 $\pm$ 0.04	0.03 $\pm$ 0.02
Chrysopidae larvae	0.08 $\pm$ 0.04	0.22 $\pm$ 0.12	0.04 $\pm$ 0.04	0.11 $\pm$ 0.04

Figure 4.1: Diagram of plot set-up for observation study. A) Two exterior plots were situated from 0 – 10 m into the field. B) Two interior plots were situated from 50 – 60 m into the field. All plots were 50 m away from all other field edges. C) Expanded view of plot demonstrated random selection of plants for aphid infestation. D) Caged plants located in between plots were used to account for mortality in the absence of predation.

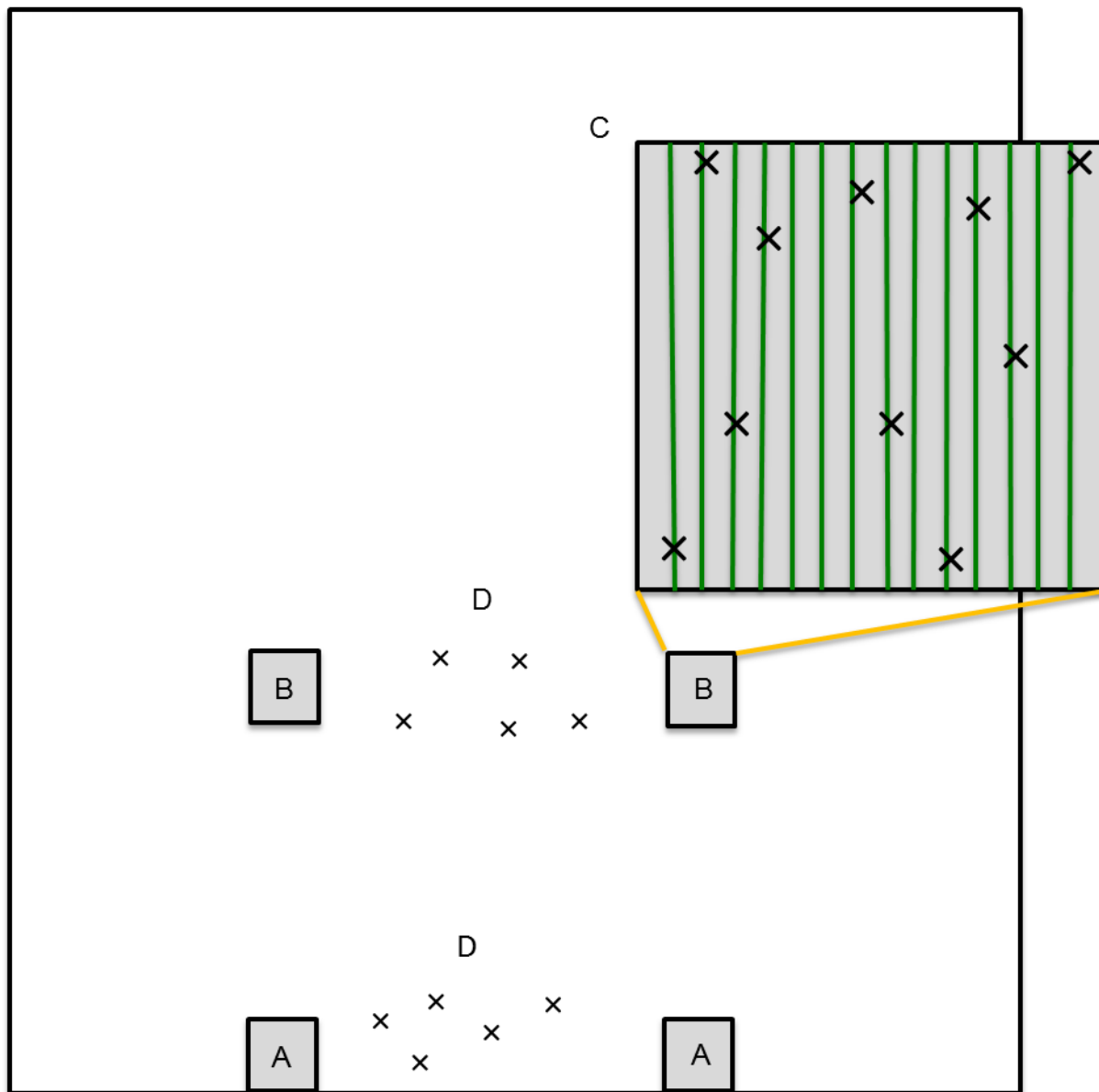


Figure 4.2: Video observation set-up. A) Aphids and natural enemies were recorded with video surveillance cameras suspended from PVC frames. B) 8 cameras were arranged radially around a DVR. C) The DVR was powered by 2 marine batteries and connected to a removable hard drive rack that allowed video files to be taken to the lab for uploading and viewing.

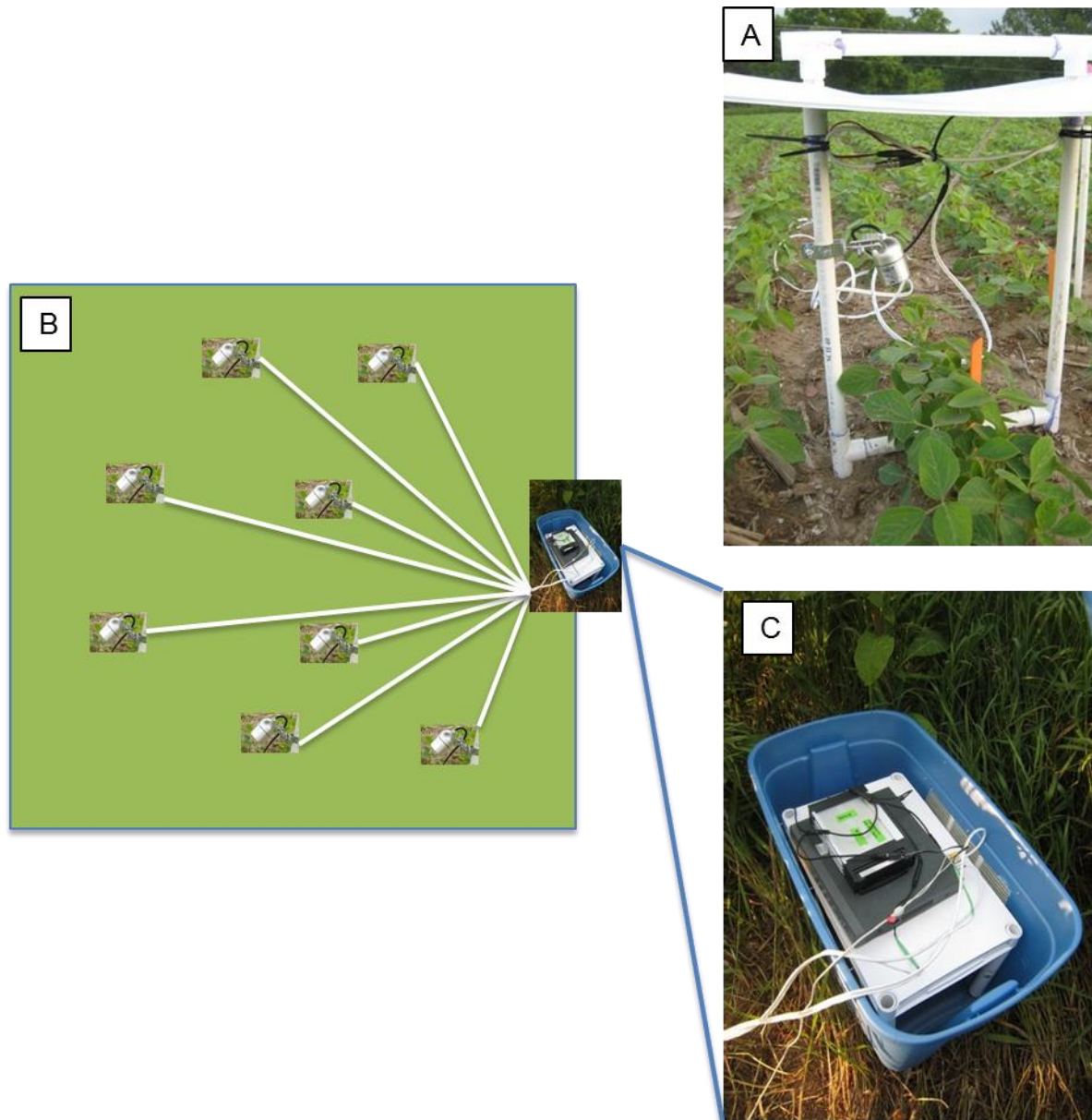
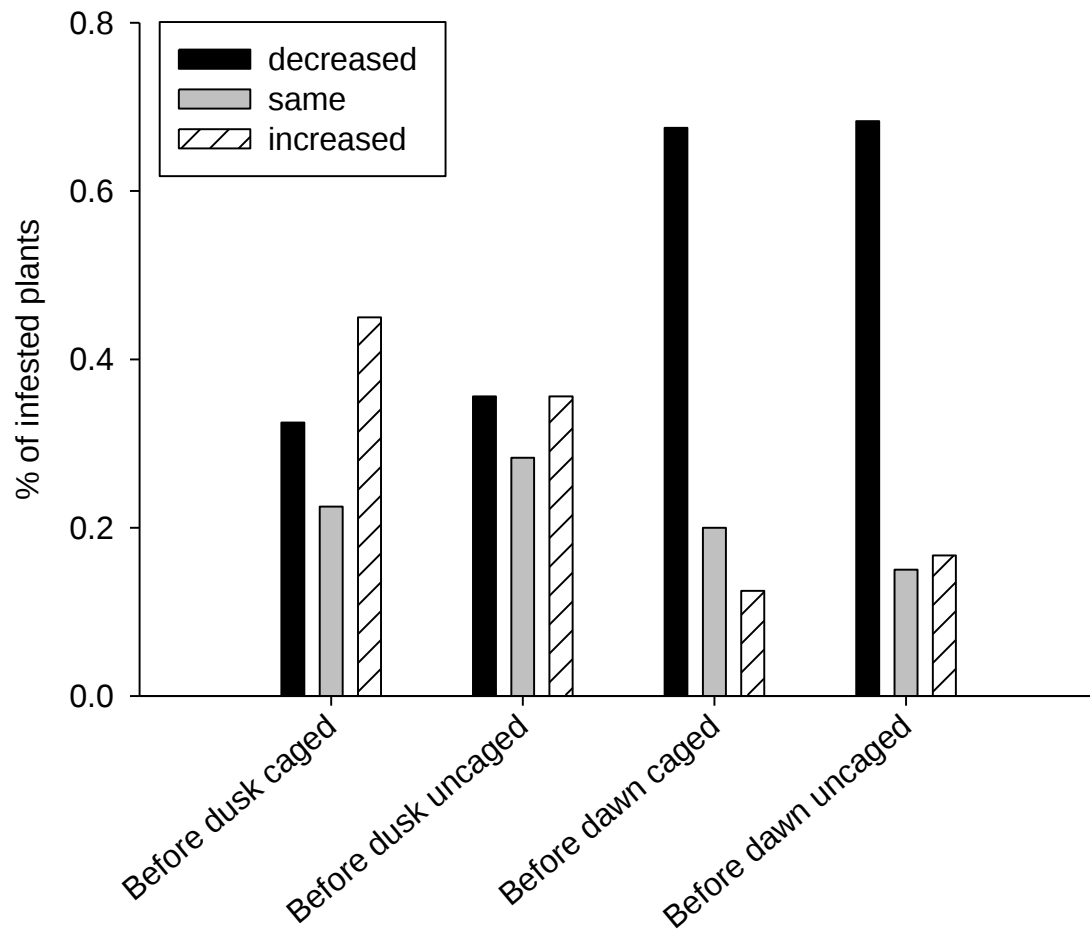


Figure 4.3: The percentage of plants on which aphid colonies decreased, remained steady, or increased within 6 h of infestation. Plants were infested prior to dusk or dawn and were caged to exclude predators or uncaged to be exposed to predators.



LITERATURE CITED

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CHAPTER V: Conclusion

Implications for managing landscapes for ecosystem services

Due to the conflicting demands for ecosystem services and limits to the land that produces them, there is increasing interest in multifunctional landscapes, i.e. those that are managed to provide multiple ecosystem services simultaneously (Romstad et al. 2000). Agricultural landscapes produce multiple services, including the provision of food, fuel and fiber, the support of soil fertility and nutrient cycling, regulation of water quality, greenhouse gas sequestration, and cultural services (Swinton et al. 2007, Power 2010). The provision of these services in agricultural landscapes is dependent upon the composition and configuration of agricultural landscapes (Goldman et al. 2007). Therefore, in order to simultaneously manage agricultural landscapes for multiple services, we must understand the specific relationships between the physical structure of the landscapes and the services they provide. The objectives of this dissertation were to: 1) examine the effectiveness of habitat management for soybean aphid biological control in landscapes of varying complexity, 2) to examine in detail specific aspects of landscape structure that influence coccinellid abundances, 3) to examine the influence of coccinellid immigration on soybean aphid suppression, and 4) assess diel variation in the soybean aphid natural enemy community.

Insect-mediated services like pollination and biological control are dependent upon the insect communities. In this work, I contributed to a growing body of evidence that important natural enemy communities are influenced by landscape structure (Chaplin-Kramer et al. 2011). I found that coccinellids increased with the proportion of semi-natural habitat in the surrounding landscape. Coccinellids are dependent upon semi-natural habitats for over-wintering and for foraging during periods in which prey is not available in agricultural habitats. Additionally, the

presence of alternative prey in semi-natural areas in the spring can allow coccinellids to achieve the nutritional status necessary to initiate reproduction, allowing the population to increase and contributing to greater pest control (Bianchi and van der Werf 2004).

Secondly, I have shown that coccinellid beetles utilize habitat management plantings, whether for floral resources (Harmon et al. 2000) or for alternative prey (Dong et al. 2012). However, coccinellid use of our habitat management plantings did not result in increased coccinellid activity within adjacent fields. This suggests that, while coccinellids are able to locate and use locally-provided resources, these resources may be insufficient to change population dynamics. For natural enemies like coccinellids that disperse over large distances (Hodek et al. 1993), the availability of resources at the landscape scale is likely more important for determining overall population levels, further emphasizing the need to manage for biological control services at landscape scales. Despite this result, habitat management may still be useful as a tool to increase biological control services in a given locale. Carefully timed management, such as cutting the habitat management strip at a key time for aphid suppression, could force the coccinellids using the strip to disperse into the adjacent crop (Dong et al. 2012).

Third, I demonstrated that the arrival rate of coccinellids at patches infested with soybean aphids can be critical to prevent aphid increases. This suggests that understanding how local conditions influence that rate could provide new tools for habitat management. In systems like this, in which transient predators are important, it is not sufficient to manage for natural enemy abundance. Rather, management must also consider dispersal and foraging behaviors of those transient predators. For example, Grez and others (2010) found that different border types affect the immigration rate of coccinellids into adjacent fields, and that effects were species specific.

Several studies have suggested that habitat configuration may influence coccinellid dispersal and immigration to patches (Greze and Prado 2000, With et al. 2002, Greze et al. 2004, Zaviezo et al. 2006). However, in my examination of specific aspects of landscape-level composition and configuration that could influence coccinellids in chapter 2, I saw no strong effects of landscape-level configuration in terms of habitat interspersions on the coccinellid communities I studied. These differences are likely due to the scale at which configuration was examined. The above studies cited examining the effects of habitat fragmentation and isolation on coccinellid dispersal were primarily conducted within small patches (200-900 m²), suggesting that these conditions influence coccinellid dispersal behavior at small scales. In contrast, overall abundance of coccinellids is likely determined by resource availability at larger scales.

Finally, natural enemy communities within soybean fields vary throughout the diel cycle. Additionally, the foraging rates of natural enemies, and their subsequent encounters with pest individuals, may not be well-reflected by sampling methods that measure relative abundance. The activity-density and species richness of several of the taxa most actively foraging at night are well known to be dependent upon landscape structure (e.g. spiders (Clough et al. 2005, Isaia et al. 2006, Oberg et al. 2007, Drapela et al. 2008); carabids (Bommarco 1998, Varchola and Dunn 1999, Aviron et al. 2005, Purtauf et al. 2005, Werling and Gratton 2008); and Opiliones (Gardiner et al. 2010)). This suggests that intentional landscape management to improve pest suppression will likely have to consider the effects on multiple natural enemy taxa simultaneously.

Context dependence of landscape effects

While this and other studies consistently emphasize the importance of landscape scale in ecosystem service management, the contradictory nature of some studies indicates the context

dependence of these effects. For example, considering only coccinellid beetles, studies have found surprisingly different patterns. In addition to the work presented here, others have found increases in coccinellid abundance with increasing abundance of semi-natural habitat in the landscape, specifically in field crops like soybean (Gardiner et al. 2009) and corn (Elliott et al. 2002). In contrast, several researchers have found increases in coccinellids with the amount of crop habitat in the landscape, specifically in nettles (Rand and Tschardtke 2007) and organic cereal fields (Caballero-Lopez et al. 2012). These seemingly contradictory results are possibly the result of: 1) the nature of the habitat where beetles were collected, in comparison to surrounding landscape; 2) the changing relationships between various landscape variables in different sets of landscapes.

Regarding the first point, the abundance of a particular natural enemy captured in a given habitat will depend both on the overall abundance of that natural enemy in the surrounding landscape and the natural enemies preference for that habitat. Natural enemies may be found in greater abundance because there are simply more of them available to colonize that habitat. On the other hand, natural enemies may colonize a habitat disproportionately to their overall abundance if they have a strong preference for that habitat. For example, syrphids locally show a preference for floral habitats over grass habitats, but also show increased densities in the floral habitats as cropland in the surrounding landscape increased (Haenke et al. 2009). This result is not because syrphid densities are necessarily higher in agriculturally-dominated landscapes, but rather that syrphids may concentrate in floral resources when there are fewer other resources to utilize in the surrounding landscape. Others have found responses of ground-dwelling predators to landscape structure on conventional but not organic farms (Weibull et al. 2003, Schmidt et al. 2005). This suggests that on conventional farms where resources are likely to be insufficient for

natural enemies, the occurrence of natural enemies is dependent upon how many are supplied by the landscape, while organic farms may provide all of the resources necessary for natural enemies to complete their life cycles, thus their abundance may be independent of surrounding conditions. These examples indicate that on the one hand, the preference of a natural enemy for a resource-rich habitat may depend upon the amount of resources available in the landscape, while on the other hand, the abundance of natural enemies within a resource-poor habitat may depend upon the ability of the landscape to supply those natural enemies. Future work examining these context dependencies will be necessary to understand under what conditions landscape and local management actions are expected to be most effective for increasing biocontrol services from natural enemies.

A second mechanism for the context-dependence of natural enemy-landscape relationships is the differing relationships between variables in different sets of landscapes. For example, Werling et al. (2011) found decreases in the abundance of exotic coccinellids in corn, switchgrass and prairie habitats with increases in herbaceous perennials like hayfield and pastures. In contrast, a similar metric encompassing hayfields and pastures was not correlated with coccinellid abundances in this work. Similarly, several studies have found relationships between natural enemies and overall habitat diversity (Thies and Tscharntke 1999, Steffan-Dewenter et al. 2002, Roschewitz et al. 2005), while I found no relationship. In such cases, natural enemies may be responding to a particular variable that is correlated with another variable in one set of landscapes but not in others. In the case of habitat diversity, in studies in which this metric was correlated with natural enemies, it was also correlated with amount of semi-natural habitat, while in my work those two landscape variables were not related. Therefore, selecting a single variable could lead to inappropriate interpretations of results. In this

work, I have shown that multiple landscape variables, all of which could reasonably affect coccinellid biology, were all highly correlated with one another. This emphasizes the need to more carefully examine all aspects of landscape, as opposed to using single metrics whose relationships with other metrics may differ across landscapes and regions.

Additionally, a focus on single, broad metrics may over-look important “hidden heterogeneity” within agricultural landscapes that could have important implications for natural enemies (Vasseur et al. 2013). A given crop may be managed in a variety of different ways, including nutrient regimes, use and choice of pesticides, and timing and choice of tillage practices. These differences can drastically affect the quality of a crop habitat for natural enemies and other taxa. For example, a reduction in fertilizer use resulting in decreased availability of aphid prey can have greater impacts on coccinellid populations than altering landscape composition (Bianchi et al. 2007). Because crop management is more directly under farmer control than other aspects of landscape heterogeneity, an increased research focus on this area could yield more easily applicable management tools.

Expanding to underrepresented regions and agroecosystems

The context dependence of natural enemy relationships to landscape suggests an urgent need to recreate these kinds of studies in other agroecosystem types and in under-represented parts of the world. The majority of this type of research has been conducted in the temperate climates in the northern hemisphere (i.e. in Europe and the United States), where most semi-natural habitats consist of grasslands and forests. Even amongst these regions, differences exist. Europe and the United States also have different agricultural histories. Agriculture spread slowly across Europe thousands of years ago (Pinhasi et al. 2005). With agriculture being an integral part of the landscape over such a long period of time, agroecosystems can actually support

substantial biodiversity and policies are in place to encourage agricultural practices that continue to support biodiversity, e.g. Agriculture Environment Schemes, (Kleijn et al. 2011). In contrast, the midwest and western U.S. was settled intentionally, systematically, and comparatively rapidly. Agricultural intensification in these regions took place over periods of a few hundred rather than thousands of years, giving species less time to adapt to agroecosystems. Thus, the more intensified agricultural landscapes in the U.S. could result in lower natural enemy abundance, as has been postulated for lower spider density in U.S. than European crop fields (Nyffeler and Sunderland 2003).

Other agricultural regions around the world likely have even greater differences in the degree and history of intensification, crops grown and agronomic practices utilized, and the identity of both pest and beneficial species living within agroecosystems. We are aware of a handful of landscape studies conducted outside of Europe and the U.S., including in arid agroecosystems in the Middle East (Pluess et al. 2010) and in tropical agroecosystems in Asia (Wilby et al. 2006). Many of the regions under-represented by this type of research also have some of the fastest growing populations in the world and will likely have the greatest increases in demands for food production in the near future (Tilman et al. 2011). As a consequence, these areas will experience rapid changes in landscape structure as natural areas are converted for food production. Research that would inform land management to preserve ecosystem services in these regions in the face of these changes is critical.

Finally, agriculture is not limited to rural areas within a matrix of remaining semi-natural habitat. Recently, much attention is being paid to urban agriculture as a means to address social justice and food security issues in urban areas (Grewal and Grewal 2012). Until recently, there has been little examination of arthropod biodiversity in urban areas, and much of that is limited

to surveys within different habitats (McIntyre 2000). Yet urban areas have the potential to produce numerous ecosystem services, and there is a need to better understand the relationship between urban and residential landscapes and the ecosystem services they provide (Cook et al. 2012, Jansson 2013). Research examining the ability of urban arthropod communities to provide pollination and pest suppression services for urban food production is needed. This and other urban ecosystem service work will be critical for urban sustainability planning, especially as 70% of the world's population is expected to live in cities by 2050 (World Health Organization 2013).

Overall it is clear that landscape structure is integral to support natural enemy communities and provision of pest suppression services. Continued study of these relationships, including their context-dependence and amenability to manipulation, may yield information critical to the future design of such landscapes for intentional provision of multiple ecosystem services. Understanding how these relationships are, or are not, generalizable across ecosystems and regions will be necessary to apply this knowledge on a global scale.

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