

**SOYBEAN APHID SUPPRESSION AND NATURAL ENEMY MOVEMENT IN
AGRICULTURAL LANDSCAPES IN MANITOBA**

By

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**A Thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfilment of the requirements for the degree of**

MASTER OF SCIENCE

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ABSTRACT

Landscape complexity and arthropod predators have been shown to play a major role in suppression of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) in North America. I examined the impact of landscape complexity and patterns of predator movement between habitats on sentinel soybean aphid populations in 27 soybean fields in Manitoba over a two-year period. Predator movement was quantified using bi-directional Malaise traps and mark-release-recapture experiments. My results revealed that there was a strong to moderate suppression of soybean aphids across the gradient of landscape complexity studied. I found that predator movement between soybean and adjacent habitats was as important as landscape characteristics in explaining aphid suppression. My results indicate that the direction of predator movement in soybean field borders is influenced by the type of adjacent habitat and by predator identity. My findings highlight the importance of pest control services provided by aphidophagous predators in agricultural landscapes.

ACKNOWLEDGEMENTS

I extend my sincere gratitude and appreciation to the many people who made this study possible. With a deep sense of gratitude, I express my thanks to my advisor, Dr. Alejandro C. Costamagna for his patience, informative field trips, collection of samples, insect identification, landscape and statistical analysis, and for all the ‘advice’ he has attempted to bestow upon me.

I am very grateful to my advisory committee members, Dr. N.J. Holliday, Dr. Peter G. Mason, and Dr. David Walker, for their guidance and criticisms at the various stages of this project, and their examination of my thesis.

I would like to thank Jordan Bannerman for his field and laboratory assistance, insect identification, statistical advice on R software, and reviewing earlier stages of my thesis.

I also offer my sincere gratitude to Dave Holder, Lisa Babey, Cherilyn Babel, Melanie Scallion, Diana Dunlop, Aldo Rios, Dr. Tharshi Nagalingam, Arash Kheirodin, Alicia Leroux, Kaitlyn Patterson, Mikala Epp, Liane Carter, Zoe Rempel, Leonardo G. da Silva, Calvin Dick, Brian Miller, Crystal Almdal, and Corey Blad for their various contributions to this project, including field and laboratory assistance.

I would like to thank Brian Miller for his guidance in landscape mapping using ArcGIS software for this project.

Thanks also to the staff and students of the Entomology Department for their various contributions to this thesis.

I am grateful for the University of Manitoba's Glenlea Research Station, Ian N. Morrison Research Facility at Carman, and several soybean farmers in Manitoba for their permission to conduct this project in soybean fields.

I would like to thank Dr. John Gavloski and Dennis Lange for their help in finding commercial soybean fields, and for providing necessary information on soybean growing in Manitoba and on soybean pests.

I am very grateful to the following taxonomists: Dr. Jeff Skevington and Andrew D. Young (Canadian National Collection of Insects, Arachnids and Nematodes), for their help with identification of hover fly species, and Dr. J.A. Garland (Canadian National Collection of Insects, Arachnids and Nematodes) for his help with identification of green lacewing species.

I am thankful for the financial assistance provided through grants awarded to Dr. Alejandro C. Costamagna from the Manitoba Pulse and Soybean Growers Association, the Agri-Food Research and Development Initiative (ARDI), and the NSERC Discovery Program.

I am grateful for the personal funding that I received, including a University of Manitoba Graduate Fellowship, a University of Manitoba International Graduate Student Entrance Scholarship, an Entomological Society of Manitoba Graduate Scholarship, a University of Manitoba Graduate Student Association Conference Award, a University of Manitoba Faculty of Graduate Studies Travel Award, a Masters’ level Outstanding Student Award from the International Organization for Biological Control, a Dr. Lloyd M. Dosdall Memorial Scholarship from the Entomological Society of Canada, and an International Branch Graduate Student Award from the Entomological Society of America.

Last, but not least, a warm appreciation goes to my parents, my brother and sister-in-law, my wife Udari Wanigasekara, and her parents for their never ending love and encouragement.

This thesis is dedicated to all my teachers, for their support and encouragement during the challenges of my life.

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CHAPTER 1: INTRODUCTION

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is native to Asia and an important pest of soybean, *Glycine max* (L.) Merr. (Fabaceae) in Asia and North America (Wu et al. 2004; Ragsdale et al. 2011). Soybean aphid was first detected in the United States in 2000 (Venette and Ragsdale 2004), and by 2001 it was found in three Canadian provinces: Ontario, Québec, and Manitoba (Brodeur et al. 2000; Gavloski 2002; Hunt et al. 2003). In Manitoba, severe outbreaks of soybean aphids were observed in 2006 and 2008 (Gavloski 2006; Gavloski 2008). In North America, soybean aphids can cause up to 40% yield reductions in soybean and have led to widespread insecticide applications (Ragsdale et al. 2007; Ragsdale et al. 2011; Tilmon et al. 2011). In Manitoba, soybean is a major crop; approximately 0.5 million ha were seeded and 1.4 million metric tons of soybean were harvested in 2015 (Statistics Canada 2015). To manage future outbreaks, it is important to determine factors regulating soybean aphid populations in Manitoba.

Numerous studies indicate that diversity, complexity, and composition of the surrounding landscape influence the diversity and abundance of natural enemies that have the potential to decrease pest populations in crop fields (Marino and Landis 1996; Elliott et al. 1998; Landis et al. 2000; Thies et al. 2003; Tscharrntke et al. 2005; Bianchi et al. 2006). Specifically, Gardiner et al. (2009a) and Woltz and Landis (2013) found that landscapes in the Midwestern United States that are dominated by soybean and corn monocultures have reduced levels of biological control of soybean aphids. Since agricultural landscapes in Manitoba differ from typical US Midwestern conditions, most notably by the high prevalence of canola and cereals (i.e. wheat, oat and barley) as dominant annual crops (Manitoba Agricultural Services Corporation 2016), it is important to determine the role of landscape complexity in the suppression of soybean aphids in this region. Movement patterns of natural enemies across the agricultural landscape are important for pest

control services (Schellhorn et al. 2014), and these patterns can help to identify the habitats that act as sources of these natural enemies (e.g. Macfadyen and Muller 2013).

In this thesis, I analyse the association among landscape characteristics, movement of aphidophagous predators, and soybean aphid suppression in agricultural landscapes. In addition, I quantify the direction of predator movements in soybean field borders in an attempt to identify habitats that are sources of predators. I begin with a literature review of soybean aphids, landscape complexity effects on crop pests and their natural enemies, movement of aphidophagous natural enemies in the agricultural landscape and landscape effects on soybean aphids and their predators. The two research chapters are written in paper style, addressing the above objectives. Each research chapter includes an abstract, introduction, materials and methods, results, and discussion unique to that chapter. In the general discussion, the findings from the two research chapters are related to each other, and overall conclusions are derived.

CHAPTER 2: LITERATURE REVIEW

Soybean aphids are one of the most well studied soybean pests globally, due to their wide distribution and potential to reduce yield. This chapter discusses soybean, soybean aphids and their significance as agricultural pests, the influence of landscape complexity on pest suppression and natural enemy diversity and abundance, and the movement of natural enemies and soybean aphid suppression in agricultural landscapes.

Soybean

Soybean in Asia and North America

Soybean, *Glycine max* (L.) Merr. (Fabales: Fabaceae), is native to East Asia and it has been grown in China for 4,500 years (Wu et al. 2004). Soybean was first introduced to North America from China and planted as a crop in Savannah, Georgia, in 1765 (Hymowitz and Harlan 1983). Soybean is cultivated worldwide due to its adaptability to different environments, fast growth, use for human and animal consumption, and broad medicinal and industrial applications (Wu et al. 2004). Global soybean production is predicted to increase by 2.2 % annually, with an expected 371.3 million tons being produced in 2030 (Masuda and Goldsmith 2009).

Soybean is one of the major crops in Canada. In 2015, 2 million hectares (ha) of soybeans were seeded and approximately 3.5 million metric tons were harvested (Statistics Canada 2015). In Manitoba, soybean was seeded on approximately 0.5 million ha and approximately 1.4 million metric tons of soybeans were harvested in 2015 (Statistics Canada 2015). Between 2014 and 2015, Canada exported 3.8 million metric tons of soybeans to other countries (Agriculture and Agri-Food Canada 2016). In Canada, soybean exports are worth over \$1 billion annually, and they were worth more than \$160 million in Manitoba by 2011 (Manitoba Agriculture Food and Rural Development 2012; Agriculture and Agri-Food Canada 2015). Since, soybean has become

one of the major crops in the province of Manitoba, it is important to consider the factors affecting soybean production.

Soybeans are susceptible to many abiotic and biotic conditions in the province; for example, fully grown soybean plants are sensitive to the herbicides used to control agricultural weeds (Manitoba Agriculture 2011). Soybean seeds, seedlings and mature plants are also sensitive to seed rot, frost damage, and weed competition respectively (Manitoba Agriculture 2011). Soybean yields can also be reduced by the activities of insects, that may injure one or many parts of the soybean plant at various times in the crop cycle (Kogan and Turnipseed 1987). Among the most important of these insects is the soybean aphid.

Soybean Aphids

Soybean aphid invasion and their North American distribution

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a major soybean pest, reducing soybean yields globally (Wu et al. 2004; Ragsdale et al. 2011). In North America, this major invasive species has caused significant yield losses in soybean production since its arrival (Ragsdale et al. 2004; Heimpel et al. 2010). The soybean aphid was first detected in 2001 in several areas around the Great Lakes in the United States and had spread to 30 U.S. states by 2009 (Venette and Ragsdale 2004; Mignault et al. 2006; Ragsdale et al. 2011). In Canada, the soybean aphid was first detected in Ontario in 2001 (Hunt et al. 2003) and was recorded for the first time in Emerson, Manitoba in 2001 (John Gavloski, personal communication). Soybean aphid population outbreaks were reported in 2006 and 2008 in Manitoba (Gavloski 2006; Gavloski 2008), but severe outbreaks in the province have not been reported since.

Soybean aphids: their hosts and life cycle

Soybean aphids are heteroecious holocyclic species (i.e. species that alternate their hosts and sexually reproduce during their life cycle). They use buckthorn (*Rhamnus* spp.; Rosales: Rhamnaceae) as their primary host for overwintering and soybean as their secondary host during the growing season (Ragsdale et al. 2004). *Rhamnus davurica* Pallus and *Rhamnus japonica* Maximowicz are the most common overwintering hosts in China and Japan (Takahashi et al. 1993). In North America, the most common overwintering hosts are *Rhamnus cathartica* L. (common buckthorn), *Rhamnus alnifolia* L'Hér. (native alderleaf buckthorn), and *Rhamnus lanceolata* Pursh (Rosales: Rhamnaceae) (Voegtlin et al. 2004; Voegtlin et al. 2005; Ragsdale et al. 2011). In Québec and Ontario, soybean aphid overwinters on *R. cathartica* (Bahlai et al. 2007; Rhinds et al. 2007; Bahlai and Sears 2009; Bahlai et al. 2010), but in Manitoba it may not overwinter possibly due to very low winter temperatures (Gavloski 2015b; Philip 2015), and field colonization of aphids results from immigration from the United States as winged individuals in late July (Gavloski 2006; Gavloski 2008). Following the arrival of immigrant aphids, there are several parthenogenetic generations throughout the rest of the summer (Gavloski 2015b). Although Blackman and Eastop (2000) listed *Pueraria phaseoloides* (Roxb.) Benth. and *Desmodium intortum* (Mill.) Urb. (Fabales: Fabaceae) as secondary hosts of soybean aphids in other parts of the world, in North America, these two legumes are not commonly infested by soybean aphids, and therefore play a minor role in soybean aphid population dynamics.

In the Midwestern United States, overwintered eggs hatch into nymphs and develop into wingless fundatrices (i.e. parthenogenetic viviparous female aphids that emerge in spring from the overwintered eggs), from March to May (Ragsdale et al. 2004). Several generations may be

produced on *Rhamnus* spp., until winged spring migrants migrate into soybean. While on soybean, both wingless and winged morphs are produced through parthenogenetic reproduction, resulting in many overlapping generations. When temperature and photoperiod decrease in the fall, female alates (gynoparae) are produced which then produce both male and female offspring. Then these gynoparae migrate to the overwintering hosts, *Rhamnus* spp., and produce nymphs that develop into oviparae that can feed on the primary host. Meanwhile, winged males are produced on soybean and migrate to *Rhamnus* spp. to mate with oviparae. After mating, oviparae deposit eggs on twigs along the margin of buds of *Rhamnus* spp. and begin the overwinter process (Ragsdale et al. 2004; Wu et al. 2004).

Soybean aphids: injuries to soybean and economic threshold

Feeding by soybean aphids results in the removal of photosynthates of the soybean plant and disruption of photosynthesis (Macedo et al. 2003; Van Emden and Harrington 2007). Feeding injury may result in reductions in plant height, pod number, seed number per pod, and seed size (Wang et al. 1995; Beckendorf et al. 2008). Consequently, at high aphid densities, yields decrease and the seed-oil content drops (Beckendorf et al. 2008). Reduced yield and seed quality may occur due to plant viruses carried by soybean aphid vectors, such as *Soybean mosaic virus* (SMV), *Alfalfa mosaic virus* (AMV), *Tobacco ringspot virus* (TRSV), *Potato virus Y* (PVY), *Potato leaf roll virus* (PLRV), *Cucumber mosaic virus* (CMV), and *Indonesian soybean dwarf virus* (ISDV) (Iwaki et al. 1980; Hill et al. 2001; Clark and Perry 2002; Davis et al. 2005; Davis and Radcliffe 2008; Nault et al. 2009). Soybean aphids have the potential to transmit some of these viruses to other crops, such as snap beans (Nault et al. 2009), seed potatoes (Davis et al. 2005; Davis and Radcliffe 2008), and squash (Ragsdale et al. 2011).

Since 2001, soybean aphid damage has resulted in significant economic losses in North America with yield losses of up to 40 % in the mid-western USA (Ragsdale et al. 2004; Ragsdale et al. 2007). In addition, soybean growers regularly allocate money for scouting of soybean aphids and spraying insecticides to protect soybean yield (Ragsdale et al. 2011). Pest management decisions in Integrated Pest Management programs of agricultural pests are based on economic thresholds and the economic injury levels. The economic threshold is “the number of insects (density or intensity) that should trigger management action”, and the economic injury level is defined as “the lowest number of insects that will cause economic damage or the minimum number of insects that would reduce yield equal to the gain threshold” (Pedigo and Rice 2009). In the case of soybean aphids, the economic threshold validated for the Midwestern United States is on average 250 aphids per plant, with populations continuing to rise in the following days (Ragsdale et al. 2007). Under normal conditions this threshold give growers a week to implement the insecticide application before the aphid population reach the economic injury level of 674 aphids per plant (Ragsdale et al. 2007). This economic threshold has been validated until the R5 soybean stage; after that stage soybean plants may tolerate higher aphid densities without major yield reductions (Ragsdale et al. 2007).

Methods of controlling soybean aphid

Chemical control, increasingly in combination with resistant soybean varieties, is the most frequent methods used to control outbreaking aphid populations. Several studies have shown that non-outbreak conditions are maintained mostly by the action of natural biological control.

Chemical control

Organophosphate and pyrethroids are the most commonly used foliar insecticides for soybean aphid control in the USA (Ragsdale et al. 2007; Ragsdale et al. 2011). Both types of insecticides

are used either in aerial or ground applications in Manitoba (Manitoba Agriculture 2017b). Pyrethroid insecticides are more persistent and effective than organophosphate insecticides (Ragsdale et al. 2011). However, pyrethroid insecticides are more expensive and show insufficient activity against spider mites and therefore organophosphate insecticides are more commonly used by growers to control soybean aphids and other sap feeders such as leafhoppers, Lygus bugs and spider mites (Rice et al. 2007; Manitoba Agriculture 2017b). Johnson et al. (2008) found that both organophosphate and pyrethroid insecticides show either lethal or multiple sub-lethal effects on natural enemies, thus decreasing levels of natural control. Use of neonicotinoid treated seeds is another chemical control option available to soybean growers. Neonicotinoid compounds are only effective for the early stages of soybeans growth and do not persist long enough to provide economic control of soybean aphids at the time the crop is most susceptible to aphid outbreaks in the Midwestern United States (Johnson et al. 2009). Although there are no studies to date on the effectivity of seed insecticides to control soybean aphid in Manitoba, the results mentioned above should also apply to this region. When the economic threshold is surpassed, foliar applications of insecticides are the best way to control soybean aphids immediately; however, this method of control can have severe environmental implications, such as toxicity for non-target organisms, including humans (Aktar et al. 2009).

Resistant soybean varieties

Resistance to soybean aphids has been mainly achieved via antixenosis (i.e. plant characteristics that have negative impacts on the behaviour of herbivores) and antibiosis (i.e. plant characteristics that have negative impacts on the biology of herbivores) and genetically characterized in eight individual lines with *Rag* (Resistance to *Aphis glycines*) genes, of which five (from *Rag1* to *Rag5*) have been mapped to four chromosomes (Hesler et al. 2013). Recent

studies indicate that soybean aphid populations reach economic levels on resistant lines with *Rag1* or *Rag2* genes, but not on resistant lines with a pyramid of *Rag1* + *Rag2* genes (Brace and Fehr 2012; Hesler et al. 2013; McCarville et al. 2014). There are 18 aphid-resistant soybean lines commercially available in the Midwestern United States since 2012, 17 lines with the *Rag1* gene and one line with a pyramid of *Rag1* + *Rag2* genes (McCarville et al. 2012).

Biological control

Biological control is defined by DeBach (1964) as “the action of parasites, predators, or pathogens in maintaining another organism’s population at a lower average than would occur in their absence”. Use of natural enemies to kill or minimize pest abundance is an effective method to control pest populations naturally, including soybean aphid (Ragsdale et al. 2011). This method also has the potential to be much less expensive and more eco-friendly than chemical control methods (DeBach and Rosen 1991). There are three main approaches to biological control: classical biological control, conservation biological control, and augmentative biological control. Classical biological control is the introduction and permanent establishment of effective natural enemies from their native region to control introduced pests in new areas, and involves the importation, screening, and release natural enemies in compliance with governmental regulations (Mahr and Ridgway 1993). Conservation biological control is implementing practices to increase the effectiveness of natural enemies such as providing resources through farming and gardening practices to enhance their survival and avoiding practices that are harmful for them (Mahr and Ridgway 1993). Release of natural enemies already present in an area is termed augmentative biological control, which is important to temporally increase the natural enemy abundance to suppress the pest population in the area of release (Mahr and Ridgway 1993).

In agroecosystems, natural biological control is carried out by naturally occurring insect natural enemies that play a major role in either controlling or suppressing various pests in different crops. Based on their specificity, natural enemies can be divided into generalists, with a broad range of prey, and specialists, typically feeding on one or few species that are related (Symondson et al. 2002). Generalist predators are important for controlling pest populations because they have ability to 1) keep pace with rapid colonization under temporal and spatial disruptions, 2) exploit food resources rapidly as predators have opportunistic feeding habits, and 3) maintain their numbers when pest numbers have declined due to their ability to feed on alternative prey (Symondson et al. 2002). Among generalist predators of soybean aphid in North America, transient predators have been shown to have the most important impact (Fox et al. 2004; Costamagna and Landis 2006). Transient predators can forage over multiple plants in short periods of time and move through different habitats in their lifespan (Costamagna and Landis 2007). Transient predators can move from one infested field to another, allowing them to utilize food resources more efficiently and provide control across multiple crops (Duelli et al. 1990; Grez and Prado 2000). They can also acquire a variety of resources from different habitats in an agricultural landscape such as alternative prey, overwintering sites and protection against disturbance which affects their survival, longevity, and fecundity (Landis et al. 2000; Sutherland et al. 2001; Duelli and Obrist 2003).

Natural enemies of soybean aphid

There are at least 55 aphidophagous natural enemy taxa in Asia (Wu et al. 2004) and 43 taxa in North America (Rutledge et al. 2004). In North America, aphidophagous natural enemies in six insect orders have been confirmed to attack soybean aphids, including predators 1) Coleoptera: Carabidae, Coccinellidae, and Staphylinidae; 2) Dermaptera: Forficulidae; 3) Diptera:

Cecidomyiidae, Chamaemyiidae, and Syrphidae; 4) Hemiptera: Anthocoridae, Miridae, and Nabidae; 5) Neuroptera: Chrysopidae and Hemerobidae, and parasitoids: 6) Order Hymenoptera: Aphelinidae and Braconidae (Fox et al. 2004; Desneux et al. 2006; Mignault et al. 2006; Costamagna and Landis 2007; Ragsdale et al. 2011; Costamagna et al. 2013). Moreover, arthropods from the order Opiliones: Phalangidae and several entomopathogens like Entomophthorales and Hypocreales also attack soybean aphids (Ragsdale et al. 2011).

In Canada, few studies have been carried out to identify aphidophagous natural enemies in soybean fields. Mignault et al. (2006) conducted experiments in nine different soybean growing areas in Québec from 2002 to 2003, to characterize foliar aphidophagous natural enemies in infested fields. In their study, the most abundant natural enemies recorded were Coccinellidae, with seven lady beetle species identified. Among them, *Propylea quatuordecimpunctata* (Linnaeus) was the most common lady beetle found, followed by *Harmonia axyridis* (Pallas), *Coleomegilla maculata lengi* Timberlake, *Coccinella septempunctata* Linnaeus, *Hippodamia variegata* (Goeze), and *Brachiacantha ursina* (Fabricius) (Coleoptera: Coccinellidae) (Mignault et al. 2006). In addition, Rhains et al. (2007) found aphidophagous natural enemies in Coccinellidae, Syrphidae, Anthocoridae, and Chrysopidae in Pintendre, Québec in 2004 and 2005. Among them, lady beetles represented the most common predators and *C. septempunctata* was the most abundant lady beetle followed by *H. axyridis*. In contrast, *Orius* spp. (Hemiptera: Anthocoridae) were the dominant species found in soybean growing areas in 2010 and 2011 in Montérégie Québec, followed by lady beetles (Mitchell et al. 2014). *Nabis americanoferus* Carayon (Hemiptera: Nabidae), adult *Toxomerus* spp. (Diptera: Syrphidae), and *Plagiognathus* spp. (Hemiptera: Miridae) were the other common natural enemies found in this area (Mitchell et al. 2014).

Aphidophagous natural enemies have not been studied in soybean in Manitoba, as soybean has not been a major crop in the province until recently. However, aphidophagous natural enemies recorded in soybean in Eastern Canada can be found in other crops in Manitoba. For example, studies in Manitoba have shown that several aphidophagous species of lady beetles, damsel bugs, minute pirate bugs, green lacewings, brown lacewings, hover flies, ground beetles and parasitoids are present in alfalfa (Uddin 2005), canola (Gavloski et al. 2011) and cereals (Bakker 1974; Bakker and Robinson 1975; Gavloski and Meers 2011).

Several natural enemy manipulation studies have shown that aphidophagous natural enemies can suppress soybean aphid in North America. For example, Costamagna et al. (2008) found that final aphid population size in predator exclusion controls was 36 to 86 times greater than on soybean plants exposed to naturally occurring predators for 6 weeks in Michigan. Gardiner et al. (2009a) found an average of 5.3 times higher soybean aphid population size in cages excluding predators compared to uncaged plants after two weeks in Iowa, Michigan, Minnesota, and Wisconsin. In Québec, Rhainds et al. (2007) observed 2.6 – 7.6 times higher soybean aphid densities in predator exclusion cages compared to open plants exposed to naturally occurring predators, after 6 – 9 weeks of manipulation.

Landscape structure and agroecosystems

The structure of a landscape can be characterized by the composition (i.e. diversity and quality) and configuration (i.e. spatial arrangement) of its land cover types (Burel and Baudry 2003; Fahrig et al. 2011). Complex landscapes have high percentages of perennial habitats including natural, seminatural, or non-crop land areas, and high habitat diversity relative to simple landscapes (Thies and Tschardtke 1999; Gardiner et al. 2009a; Rand et al. 2012; Rusch et al. 2013). Furthermore, complex landscapes have also being defined by a lower percentage of crop

field areas, smaller crop field sizes, longer field borders in wider hedgerows, and more wooded perimeter per unit of field area (Marino and Landis 1996; Menalled et al. 1999; Menalled et al. 2003; Landis et al. 2008; Jonsson et al. 2012). Complex landscapes also typically have higher abundance and more taxa diversity, including natural enemies (Duelli and Obrist 2003; Bianchi et al. 2006; Chaplin-Kramer et al. 2011), which can result in greater pest suppression (Kruess and Tscharntke 1994; Gardiner et al. 2009a; Werling and Gratton 2010; Gagic et al. 2011).

Landscape structure and pest suppression

In a review of the literature, Bianchi et al. (2006) concluded that pest pressure is lower in complex landscapes that have a higher proportion of non-crop habitats when compared to simple large-scale agricultural habitats. Natural, seminatural, and non-crop areas in agricultural landscapes have negative associations with the abundance of various pest species. For example, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae), *Hypena scabra* (Fabricius), and rape pollen beetles *Brassicogethes aeneus* (Fabricius) (Coleoptera: Nitidulidae), are less abundant and cause less damage in oilseed rape crops, *Brassica napus* L. (Brassicales: Brassicaceae) in complex landscapes (Thies and Tscharntke 1999; Summerville 2004). Similarly, the number of thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), in leek fields, *Allium porrum* L. (Asparagales: Amaryllidaceae) decreases with increases of woodlands in the surrounding landscape (den Belder et al. 2002). Chaplin-Kramer and Kremen (2012) found decreasing densities of the cabbage aphid, *Brevicoryne brassicae* (Linnaeus) (Hemiptera: Aphididae), in broccoli fields at increasing proportions of natural and seminatural habitats in the agricultural landscape. These negative associations could be due to direct effects of landscape structure on pest populations, such as interference with field colonization or indirect effects, such as increasing the diversity, abundance, or availability of natural enemies (Schellhorn et al. 2014).

The influence of landscape complexity on natural enemy abundance and diversity

Increasing natural enemy diversity and/or abundance is generally associated with increased landscape complexity (Bianchi et al. 2006; Schmidt et al. 2007a; Werling and Gratton 2008; Gardiner et al. 2009a; Gardiner et al. 2009b; Chaplin-Kramer et al. 2011). Different types of non-crop habitats in the landscape may influence natural enemy populations differently however. For example, Bianchi et al. (2006) found that enhanced natural enemy activity is associated more often with the proportion of herbaceous habitats (e.g. fallows and field borders) than the proportion of woodland habitats in the landscape. A study in Wisconsin indicates that carabid beetle diversity in potato fields increases with increased proportion of natural areas in the surrounded landscape at the spatial scale of 1.5 km (Werling and Gratton 2008). Schmidt et al. (2007a) found that diversity and density of wolf spiders (Araneae: Lycosidae), long-jawed spiders (Tetragnathidae), crab spiders (Thomisidae), and dwarf sheet spiders (Hahniidae) in wheat fields show positive associations with the proportion of non-crop habitats in agricultural landscapes in Germany. Another study in Germany shows that abundance of sheetweb spiders (Araneae: Linyphiidae) in winter wheat increases with increasing proportion of grassland and non-crop habitats in the landscape (Schmidt and Tscharrntke 2005).

Natural enemy movements in agricultural landscapes

Movement of natural enemies to crops from other habitats directly affects the biological control services they provide in agricultural landscapes (Corbett and Plant 1993; Prasifka et al. 1999; Schellhorn et al. 2000). This spillover (i.e. cross-boundary subsidies of organisms) occurs from natural areas to cropping areas (Landis et al. 2000; Sackett et al. 2009) but also in the opposite direction (Rand and Louda 2006; Rand and Tscharrntke 2007; Gladbach et al. 2011). Primary

productivity of habitats, aggregative responses to high prey densities, and disturbances all influence the direction and amount of natural enemy spillover (Muller and Godfray 1997; Bong et al. 2013; Frost et al. 2015). In order to provide effective suppression of pest populations, natural enemy spillover from source habitats to crops should have sufficient number of natural enemies moving at the appropriate time (Settle et al. 1996; Landis and van der Werf 1997; Costamagna et al. 2015). In addition, meteorological and weather conditions (temperature, humidity, barometric pressure, wind speed, and direction) may influence the initiation or termination of natural enemy movements (Schellhorn et al. 2014).

Colonization of a patch (i.e. “an area containing resources that are spatially or temporally aggregated and separated in space and time from other areas containing that resources”) by natural enemies involves three processes: detection, arrival, and settling on the patch (Schellhorn et al. 2014). Prey density and the internal state of natural enemies (e.g. hunger level) influence the immigration of these natural enemies (Schellhorn et al. 2014). Emigration of natural enemies involves leaving the patch throughout the cropping season, due to several internal and external factors (Schellhorn et al. 2014). These internal factors include sex and mating status of natural enemies, and external factors include crowding, cues from conspecifics (i.e. an insect from the same species), and heterospecifics (i.e. an insect from different species). Habitat features at the plant or patch level also influence the patch leaving behaviour of natural enemies (Schellhorn et al. 2014).

Natural habitats tend to provide more stable and heterogeneous environments than annual and arable crop habitats (Tscharrntke et al. 2007). Rapid colonization of natural enemies from adjacent natural habitats helps to effectively control pest populations in nearby crops (Duelli and Obrist 2003; Schellhorn et al. 2014). Studying natural enemy movements between crops and

adjacent habitats is necessary for predicting pest suppression in crop fields and to improve pest management decision making in modern agricultural systems.

There are only a few studies that have quantified natural enemy movements between habitats directly (Duelli et al. 1990; Macfadyen and Muller 2013; Macfadyen et al. 2015; González et al. 2016). In Switzerland captures on sticky cards showed that emigration of lady beetles from corn fields to adjacent barley and wheat fields is higher than immigration to corn fields, and captures from directional pitfall traps indicated that carabid beetles have higher immigration into corn from adjacent wheat and barley fields compared to emigration (Duelli et al. 1990). In Australia, Macfadyen and Muller (2013) using bi-directional malaise traps, found that parasitoids move in greater numbers from natural vegetation to canola fields than vice versa, but predators do not show differences in their movement between native perennial vegetation and canola fields. In another study using bi-directional malaise traps, Macfadyen et al. (2015) revealed that both predators and parasitoids move into wheat crops from natural areas. A study in central Argentina demonstrated that coleopteran predators move in greater numbers into soybean from adjacent forests than in the opposite direction (González et al. 2016). However, in the same study, abundance of total natural enemies (combined Coleoptera, Diptera and Hymenoptera) did not show a directionality of movement between forest and soybean habitats (González et al. 2016). In addition, Grez et al. (2010) studied lady beetles at borders of alfalfa with adjacent vineyards, corn, and annual vegetables in Central Chile using double-sided sticky traps and found that abundance and species richness are not affected by the type of adjacent habitats. Despite this recent progress, patterns of movement of natural enemies within agricultural landscapes are still poorly studied.

Landscape structure and soybean aphid suppression

Using predator exclusion studies replicated in Iowa, Michigan, Minnesota, and Wisconsin, Gardiner et al. (2009a) found increased soybean aphid suppression associated with higher habitat diversity, and particularly with higher proportion of forested areas and perennial grasslands in the landscape. Similarly, Noma et al. (2010) found that increasing habitat diversity in the surrounding landscape decreases soybean aphid abundance in the same four Midwest States. Gardiner et al. (2009a) and Woltz and Landis (2013) found that aphidophagous lady beetle abundance increases in complex landscapes associated with more forests and grassland areas, with smaller field sizes, and higher crop diversity around the focal soybean fields. Less diversified annual crops grown in larger fields in simple landscapes had lower lady beetle abundance (Gardiner et al. 2009a; Woltz and Landis 2013). The abundance of ground predators of soybean aphids also varies in landscape complexity. For instance, the activity density of spiders (Order: Araneae) increases in landscapes with larger proportions of forests and grasslands (Gardiner et al. 2010). In the same study, Gardiner et al. (2010) found that the diversity of carabid beetles in soybean fields increases with higher proportions of grassland habitats in landscapes. However, recent studies have also found opposite patterns. Schmidt et al. (2011) found a negative association between the proportion of grassland habitats and the abundance and variety of natural enemies of soybean aphids in Iowa. Similarly, a landscape study in Québec has shown higher soybean aphid abundance in complex landscapes compared to simple landscapes, at a 500 m spatial scale (Mitchell et al. 2014). Finally, Stack Whitney et al. (2016) found increased soybean aphid abundance with increasing forests in the agricultural landscape in Wisconsin. Altogether, these studies suggest that increased landscape complexity is not always associated with reduced aphid populations.

Studies in natural enemy movements between soybean and adjacent habitats including both crops and non-crop areas are generally lacking. Thus, identifying habitats that can act as sources of natural enemies is important for understanding and improving biological control services and pest management of soybean aphids. Since lady beetles likely provide the most effective biological control of soybean aphids (Fox et al. 2004; Costamagna and Landis 2007), it is important to learn more about their movements across the landscapes. Lady beetles engage in trivial movements (i.e. daily short trips) between adjacent habitats for “resource mapping” (Van Dyck and Baguette 2005; Hodek et al. 2012). In less diversified landscapes, alfalfa, *Medicago sativa* L., provides a reservoir for many insect natural enemies including lady beetles (Elliott and Michels 1997; Stephens and Losey 2004), that can move into other crops where they contribute to suppress pests (e.g. Schmidt et al. 2007b).

In agricultural landscapes, I hypothesize that suppression of soybean aphid populations is influenced by landscape characteristics and movement of natural enemies. Therefore, the research presented in this thesis is focussed on the following questions:

- i. Can aphidophagous predators suppress soybean aphids in Manitoba?
- ii. Does landscape complexity affect soybean aphid suppression?
- iii. Do levels of predator movement between soybean and adjacent habitats affect soybean aphid suppression?
- iv. Do models that combine both landscape and predator movement variables have better explanatory power for soybean aphid suppression than models with only landscape variables or predator movement variables?
- v. Do different adjacent habitats to soybean fields influence movement directionality (i.e. immigration and emigration) of aphidophagous predators?

vi. Can lady beetles disperse effectively between soybean and neighboring alfalfa fields?

CHAPTER 3: LEVELS OF PREDATOR MOVEMENT BETWEEN CROP AND NEIGHBORING HABITATS EXPLAIN PEST SUPPRESSION IN SOYBEAN ACROSS A GRADIENT OF AGRICULTURAL LANDSCAPE COMPLEXITY

Abstract

Landscape complexity has been shown to play an important role in determining the levels of pests and predators found in agricultural fields. Movement of predators between neighboring habitats and crop fields has rarely been quantified in agroecosystems however. Here I evaluated the relationship between agricultural landscape complexity and levels of predator movement and the suppression of soybean aphid, *Aphis glycines* Matsumura, in 27 soybean fields in Manitoba. Over a two-year period, I quantified soybean aphid suppression using predator manipulation treatments, predator movement using bi-directional Malaise traps, and landscape complexity using digital maps of the area within a 2 km radius of the focal fields studied. When aphids were exposed to predation, population growth was reduced by 73.7% on average (range: 38.3% – 95.6%) compared to aphid populations protected with predator exclusion cages. Bi-directional Malaise trap and sweep-net sampling indicated that hover flies (Diptera: Syrphidae), followed by minute pirate bugs (Hemiptera: Anthocoridae), lady beetles (Coleoptera: Coccinellidae) and green lacewings (Neuroptera: Chrysopidae) were the numerically dominant predators. Immature minute pirate bugs were the numerically dominant species found in sweep-nets and visual plant counts, followed by larval hover flies. Immature stages of damsel bugs (Hemiptera: Nabidae), green lacewings, brown lacewings (Neuroptera: Hemerobiidae) and lady beetles (Coleoptera: Coccinellidae) were found in small numbers in sweep-nets. Focal fields were located in landscapes with a range of 0.3 – 40.3% of woodland with soybean, cereals, and canola as the major land-cover types present. Final aphid population size showed a negative association with the proportion of cereals and positive associations with the proportions of woodland and field

border grass in the landscape. Levels of predator movement between soybean and neighboring habitats had negative associations with final aphid population size, and were the best predictors in the multiple regression models, either alone or combined with independent landscape complexity variables. My results provide the first empirical evidence that landscape effects on pest suppression can be explained by the contribution of predators from extra-field habitats. From a management perspective, these results suggest that higher levels of pest suppression can be achieved by designing landscapes that facilitate predator movement to crops from extra-field habitats.

Introduction

There is increasing evidence that pest suppression by naturally occurring predators is an economically important ecosystem service for the agriculture industry. For example, suppression of soybean aphid by natural enemies in four Midwestern US states was estimated to be worth \$239 million/year over the two year-period from 2007 to 2008 (Landis et al. 2008). Tillage, pesticide application, and harvesting activities frequently disrupt these services, so that if natural biological control is to occur, predators must recolonize crop fields from extra-field habitats (Wissinger 1997; Landis et al. 2000). Recolonization of crops depends on the composition and arrangement of land-cover types (i.e. landscape complexity), through its effects on the abundance, community structure and dispersal capabilities of predators (Marino and Landis 1996; Thies and Tscharntke 1999), ultimately affecting the levels of pest control observed in crop habitats (Landis et al. 2000; Bianchi et al. 2006). To date, higher habitat diversity (e.g. Gardiner et al. 2009a), higher proportion of perennial habitats (including natural and semi-natural land covers, e.g. Thies and Tscharntke 1999), and lower proportion of crop habitats (e.g.

Thies et al. 2005) are characteristics of complex landscapes that have been associated with a higher abundance and diversity of predators and higher levels of pest suppression in crops.

The movement of predators in sufficient numbers from landscape sources into crops at the appropriate time is crucial for pest suppression (Macfadyen and Muller 2013; Costamagna et al. 2015; Macfadyen et al. 2015). It is therefore important to understand patterns of predator movement since this knowledge could be used to improve biological control of pests in agroecosystems (Schellhorn et al. 2014). In general, natural and other non-crop areas are considered the main sources of predators that move into crop areas, but few studies have actually examined the movement patterns of predators into crop fields and related them to landscape complexity. Macfadyen and Muller (2013) observed that predators and parasitoids move into canola from natural vegetation and Macfadyen et al. (2015) found that predators and parasitoids emigrate from natural areas to colonize cereal crops shortly after crop emergence. Predator movement between different crops could also be important for pest suppression. For example, Bastola et al. (2016) demonstrated that continuous bi-directional interchange of *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae) between cotton and alfalfa fields is important for conservation biological control of the cotton aphid, *Aphis gossypii*, Glover (Hemiptera: Aphididae). Further improvement of our understanding of patterns of predator movement across the agricultural landscape is required to guide future efforts to enhance natural pest control services in agroecosystems (Macfadyen and Muller 2013; Schellhorn et al. 2014; Macfadyen et al. 2015).

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a major pest of soybean, *Glycine max* (L.) Merr. (Fabales: Fabaceae), causing yield losses in both Asia and North America (Wu et al. 2004; Ragsdale et al. 2011). Interactions between soybean, soybean

aphid, and its predators are influenced by the complexity of the surrounding landscape at different spatial scales. Gardiner et al. (2009a) found higher soybean aphid suppression by predators associated with increased landscape diversity at a spatial scale of 1.5 km around soybean fields located in the North Central region of the USA. Additionally, working in the same region, Noma et al. (2010) found that soybean aphid abundance decreases with increasing landscape diversity at a spatial scale of 2 km. More recently, Stack Whitney et al. (2016) demonstrated a positive association between the proportion of forest in the landscape and soybean aphid abundance in Wisconsin. In contrast, Mitchell et al. (2014) found higher soybean aphid abundance in complex than in simple landscapes in Québec. These contradictory findings have also been reported in other systems. For example, Thies et al. (2005) reports higher crop colonization by cereal aphids with increasing landscape complexity in Europe. More research is still required before landscape effects can be generalized for soybean aphid, as well as for other agricultural pests.

In North America, the most common predators of soybean aphid include several species of lady beetles, minute pirate bugs, damsel bugs, brown lacewings, and larvae of hover flies and green lacewings (e.g. Ragsdale et al. 2011). Experimental manipulations have consistently shown that these generalist predators are important for suppressing soybean aphid populations (Costamagna and Landis 2006; Gardiner et al. 2009a), resulting in increased soybean yield (e.g. Costamagna et al. 2007). Direct field observations indicate that within this assemblage of predators, transient predators (i.e. predators that forage over multiple plants in short periods of time and move through different habitats in their lifetime) are the most effective species to numerically respond to changes in aphid densities (Costamagna and Landis 2007). Transient predators have an important advantage over less mobile predators, they can fly from one infested

field to another, allowing them to utilise food resources more efficiently and provide control across multiple crops (Duelli et al. 1990; Grez and Prado 2000). However, the movement of these predators between soybean and neighboring habitats has never been quantified.

In landscape studies, the implied assumption is that each patch of the same land-cover type within a landscape contributes similarly to the provision of predators to the focal fields studied. In reality, each patch could contribute very different numbers of predators due to different levels of disturbance, agronomic actions, or, in the case of semi-natural habitats, different plant species. I hypothesized that the level of predator movement between soybean and neighboring habitats would provide a more precise measure of the contribution of each landscape to soybean aphid suppression than the typical summary landscape complexity variables used in previous studies. The purpose of this study was to determine how landscape complexity and predator movement affects soybean aphid suppression in agricultural landscapes. The specific objectives of this study were to determine 1) if predators suppress soybean aphids in Manitoba, 2) if landscape complexity is a good predictor of soybean aphid suppression, 3) if levels of predator movement between neighboring habitats predict soybean aphid suppression, and 4) if models combining both landscape complexity and predator movement variables result in better predictions of soybean aphid suppression than each set of variables independently.

Methods

Study landscapes and site selection

Field experiments were conducted in 27 landscapes at twelve localities in Manitoba (Altona, Arnes, Carman, Elm Creek, Emerson, Gimli, Glenlea, La Broquerie, Letellier, Morris, Rosewood and Warren) during summers 2013 and 2014 (Appendix I). Agricultural landscapes were dominated by soybean, cereals (wheat, *Triticum* spp. L.; oat, *Avena sativa* L. and barley,

Hordeum vulgare L.), canola, *Brassica napus* L., corn *Zea mays* L., and alfalfa, *Medicago sativa* L. (Appendix II). Fields were selected to cover a range of landscape complexity, from agriculturally dominated landscapes to landscapes with moderate levels of woodland and riparian vegetation. Average size of the focal soybean field was 72.4 ± 50.7 ha (mean \pm SD); about half of the fields were quarter sections (64 ha). The minimum and maximum distance between focal soybean fields were 4 and 200 km, respectively.

Plant preparation

The widespread use of seed treated with insecticide in commercial fields prevented the use of field plants for this study. Experimental plants were seeded three weeks prior to the field study, and were grown in greenhouse conditions (16:8 h L: D; 23° – 27 °C, and 60 – 75% RH) in square plastic pots (9 cm \times 9 cm \times 18 cm high) in the greenhouse of the Department of Plant Science, University of Manitoba. The potting mixture was made by mixing equal amounts of peat mix (Sunshine® Mix #4, Sun Gro Horticulture Canada Ltd. Seba Beach, Alberta, Canada), compost and sand by volume. Four soybean seeds were seeded near the four corners of each pot (3 cm below the potting mix level) and were watered three times per week. All plants used for field trials were in the V3 or V4 vegetative stages and were exposed to natural sunlight conditions outside the greenhouse to increase their hardiness for 2 days (8 hours/day) before field experiments. Two plants were removed from the pot before field deployment. A 30 cm bamboo stick was buried in the pot to support the two well grown plants using twist ties (Figure 1b). The use of potted plants allowed standardization of plant variety, phenological stage and soil conditions among all focal soybean fields studied.

Predator manipulation experiment

Two predator manipulation treatments were used to test predation by natural enemies using predator exclusion field cages. In each focal soybean field, ten pots with soybean plants (Figure 1a) were randomly assigned (using a table of random numbers) to either open (Figure 1b) or predator manipulation treatments (Figure 1c). Each treatment within a pair was separated by approximately 1 m, and distance between pairs of potted plants was 5 m. Transects of potted plants were set up approximately 20 m from the field border to standardize for any potential edge effect. Potted plants were buried to soil level to facilitate access of ground predators to open treatment plants. Adjacent and potentially touching plants were removed to minimize aphid movement on to field plants. Prior to establishing the predator exclusion cages, the soil around the potted soybean plant was carefully checked to ensure no predators were trapped inside the cages.

Predator exclusion cages consisted of a 0.4 m diameter \times 1 m tall tomato support wire frame (WireCraft International, Renfrew ON, Canada) covered by a sleeve of fine mesh (white no-see-um netting with 0.24 mm² openings). The bottom of the mesh sleeve was attached to the tomato frame using binder clips and then buried in the soil to secure the frame. The top of the mesh sleeve was tied and attached to a 1.5 m tall metal rod at the tomato cage height, to allow easy access to the plant during aphid counts (Figure 1c). Potted plants were watered twice every week during the 2-week experiment in 2013. In 2014, an automatic watering system was used in order to minimize any potential plant water stress and to simplify logistics. The automatic watering system consisted of a 2 L plastic bottle continuously feeding water through a cotton string enclosed in a clear vinyl plastic tube (Figure 1b). Bottles were attached to the metal rods used to secure the mesh sleeve. Fertilizer (N-P-K: 20-20-20, Plant-Prod®, Sure-Gro IP Inc.,

Brantford, Ontario, Canada) was added during the second week of the experiment to maintain plant vigor (350 ml/pot, 2 ml fertilizer dissolved in 1 L of water). Bottles were refilled with water once per week.

Sentinel aphid colonies consisted of 14 adult or near-adult soybean aphids from the laboratory colony that were manually transferred to each potted plant (7 aphids per plant) using a fine camel-hair brush (Costamagna and Landis 2006; Woltz et al. 2012). The total number of alate and apterous aphids on potted soybean plants in each treatment was assessed visually 7 and 14 days after establishment. Any predators present on the plants were recorded, and those in predator exclusion cages were removed. A total of 120 experimental aphid colonies were studied from 22nd July to 10th August in 2013, and 150 colonies from 28th July to 14th August in 2014.

Sampling field populations of soybean aphids and predators

Concurrent with the predator manipulation experiment, weekly sampling of field populations of aphids and predators was conducted using standard sweep-net (0.38 m diameter) and visual plant counts for three weeks. Five sweep-net samples (25 sweeps/sample, located on a ~ 30 m long transect; full 180-degree arc through the plant canopy) were collected within a 50 m × 50 m area near to the established predator manipulation experiment in each field, and stored in ziplock polythene bags (40 cm × 30 cm) in a freezer (-18 °C) until processing. At the same time, 20 visual plant assessments were completed on haphazardly chosen plants within the same 50 m × 50 m area to record vegetative and reproductive stages of soybean plants in each field and the numbers and stages of predators and aphids. Sampling was conducted between 22nd July and 10th August in 2013 and between 28th July and 14th August, 2014. Predators of soybean aphids were identified to family or species level when possible, using taxonomic keys and the literature (Garland 1985; Vockeroth 1992; Silveira et al. 2003; Acorn 2007; Miranda et al. 2013). Hover

fly and green lacewing species identities were confirmed by taxonomists at the Canadian National Collection of Insects, Arachnids and Nematodes. Voucher specimens were deposited in the Wallis-Roughley Museum of Entomology, University of Manitoba, Canada.

Quantification of predator movement in field borders

In order to monitor movement of aphidophagous predators between soybean and neighboring habitats, Townes style bi-directional Malaise traps were established along the nearest border to the predator manipulation treatment of each soybean field (Figure 1a; Appendix I). Trapping occurred concurrently with the predator manipulation experiment. Bi-directional Malaise traps were constructed of fine mesh and had the following dimensions: the front height was 190 cm, the back height was 110 cm and the length was 160 cm (Sante Traps, Lexington KY, US). Two collection bottles attached to the top of the long edge of the trap collected samples separately from each side. Bottles were filled with 70% ethanol (~375 ml) and changed weekly during the experiment (8-day sampling periods occasionally occurred due to rain). Samples were stored in clear polypropylene containers (0.94 L, Plastipak Industries Inc., Boucherville, Québec, Canada) with 70% ethanol and transported to the laboratory for insect identification, which was performed as described for samples of field populations. In 24 fields, one bi-directional Malaise trap was established at one of field borders. In two fields in 2013 and one field in 2014, bi-directional Malaise traps were deployed at two borders in order to increase the number of borders sampled per neighboring habitat category; catches from both traps were averaged to provide one estimate per field. Borders selected for sampling had the neighboring habitat immediately adjacent to the soybean field (i.e. without wide grass strips or roads between fields) and represented the most common land-cover types across the study. To determine the patterns of predator movement between neighboring habitats and soybeans, the adult stages of all

aphidophagous predators were counted from the samples collected during the two weeks of the experiment (i.e. including families of Chrysopidae and Syrphidae that colonize fields as nectar-feeding adults, but have aphidophagous larvae, Appendix III). A total of 120 bi-directional Malaise trap samples were processed.

Landscape structure quantification

Based on the results of previous studies (e.g. Thies et al. 2003; Gardiner et al. 2009a; Costamagna et al. 2015), the landscape within a 2 km radius of the experimental manipulations within focal soybean fields was mapped, and all land use categories at the time of the study were identified. Base maps were delineated using images from Google Earth Pro (version 7.1.2.2041, Googleplex, Mountain View, California, USA) and were ground verified. GPS coordinates for the location of sentinel colonies in each field were collected using a handheld GPS receiver (Garmin eTrex Venture[®] Cx, Garmin International, Inc., Olathe, Kansas, US) and used to center digital maps. Maps from Manitoba Land Initiative (http://mli2.gov.mb.ca/mli_data/index.html) were used as digital templates to which land cover information for each landscape was added using ARC GIS 10 (ESRI 2010). Thirty land use categories were identified and classified into 12 major land-cover types: soybean, cereals, canola, corn, alfalfa, woodland, riparian vegetation, field border grass, grass forage, other crops, pasture and shrubland (Appendix II). Land-cover types representing less than 1% of the area, present in few landscapes, or not considered a source of aphidophagous predators (water bodies, urban, etc.), were not included in statistical analyses (Appendix II). Landscape complexity was estimated with Simpson's diversity index ($1 - D$), evenness, and habitat richness (Simpson 1949), using the *Vegan-Community Ecology package* in R (Oksanen et al. 2015; R Development Core Team 2016).

Analysis

Natural log-transformed (ln) soybean aphid counts were used in the analyses to meet normality and homogeneity of variance assumptions. Normality of the data was visually checked using normal Q-Q plots from the models and homogeneity of variance was visually checked using heteroscedasticity plots (fitted values vs. residuals). All statistical analyses were completed using R version 3.2.1 (R Development Core Team 2016). Variables that had zero counts had 1 added to all values before applying the ln transformation (i.e. $\ln(\text{soybean aphid} + 1)$). Unless otherwise indicated, all reported values are mean \pm SEM; $\alpha = 0.05$ was used to determine significant differences.

Predator manipulation experiment

The strength of predation on soybean aphid colonies was assessed by comparing predator exclusion cages with the open plant treatments using a split-plot ANOVA. Field, predator manipulation treatment (predator exclusion and open), and week were included as fixed factors in the model and week was modeled as a repeated-measures factor. Field was modeled as the whole-plot factor and predator manipulation was modeled as the subplot factor. Replicates within each field were considered as a random factor nested in field and predator manipulation. Fields were used as a fixed factor to test for the field \times predator manipulation treatment interaction, which can indicate different predation levels in different landscapes. One-way ANOVA was used to compare different fields for the numbers of soybean aphids captured in sweep-net samples and numbers observed in visual plant counts.

Landscape and predator movement models

Multiple linear regression analyses were used to explore the relationships between final aphid population size under predation with landscape complexity and predator movement patterns. In

all models, final aphid population size in the open treatment (the mean number of soybean aphids per pot in each field at the end of the second week) was included as a dependent variable and final aphid population size in the predator exclusion treatment was included as the first predictor, to control for any environmental effects on final aphid population size associated with each landscape and year of study. Using this base model, three different set of models were constructed.

The first set of models included only landscape variables as predictors, including total percentage area of the twelve major land-cover types (Appendix II), and habitat diversity, evenness and richness. The second set of models included only predator movement variables estimating the average movement of the most commonly collected aphidophagous taxa (Appendix III). A paired-*t* test showed no difference in immigration versus emigration movement rates (see results), and therefore both estimates were pooled for analysis to better reflect the overall patterns of insect movement between different neighboring habitats and soybean. Estimates of predator movement consisted of the number of insects captured in the bi-directional Malaise traps in each field, averaged over the capture period (i.e. either 14 days or 15 days). The low number of predators captured in sweep-net samples and visual plant counts prevented their use in multiple regression models. Finally, the third group of models were constructed by combining significant landscape and predator movement variables from the previous two sets of models.

Initial models for each of the three variable sets contained all measured variables that were not correlated (Pearson's correlation coefficient, $p > 0.05$) to avoid collinearity (Neter et al. 1996). Therefore, to utilize all the independent variables measured, different initial models combining uncorrelated variables were tested for each dependent variable analyzed. Stepwise

backward selection was used to select the best final models, retaining variables that minimize Akaike Information Criterion (AIC), using the step function in the lm procedure in R (R Development Core Team 2016). In this process, the independent variable with the highest AIC value and the highest p -value was dropped from the model in each step until the best fitted model with minimum AIC was obtained. AIC balances the amount of variation explained and the number of variables included in the model. AIC corrected for low number of observations (AIC_c) were used to select the best-supported model from the three model groups, due to the relatively small sample size of the study (Burnham and Anderson 2002). For all models, AIC_c , log-likelihood, adjusted r^2 , Akaike weights (w_i), p -value, and partial correlation coefficients of model variables are presented. Also, only significant models which had substantial support of the data (i.e. with $\Delta i < 2$, $\Delta i = AIC_c$ of model $i - AIC_c$ best model) are presented for each group of models. Akaike weights were used to illustrate the support of each model within a group of models (w_i : 0 – 1, higher values indicate higher support; Burnham and Anderson 2002). Partial correlation coefficients were used to determine the strength and direction (i.e. either positive or negative) of the relationship between aphid numbers in the open treatment and each predictor variable. Partial residuals were also used to illustrate the relationships between predictors and final aphid population size in the open treatment when all the other variables in the model were controlled. A complete list of all significant models fitted is available in Appendix IV.

Landscapes did not overlap within-year, but ten landscapes overlapped at the spatial scale of 2 km between years. Consequently, potential spatial autocorrelation was assessed for the residuals of the most supported models in each group of variables (i.e. landscape, predator and combined models) using Moran's I (Moran 1950; Paradis 2011).

Results

Predator manipulation experiment

After two weeks of exposure, aphid sentinel colonies in the open treatment were reduced by 73.7% on average (range: 38.3% – 96.5%) compared to final aphid population size in the predator exclusion treatment (Table 1; Figure 2). Although the number of aphids had increased in both open and predator manipulation treatments by the second week of the experiment, the rate of increase was higher in the predator exclusion treatment, as shown by a significant predator manipulation \times week interaction (Table 1; Figure 2). The number of soybean aphids varied among fields and increased differently among fields each week (Table 1). More importantly, the level of aphid suppression differed among fields and there was a marginally significant three-way interaction among field \times predator manipulation \times week (Table 1), indicating different rates of population increase from week 1 to week 2 in the two treatments among the fields studied. Negligible numbers of alate aphids (average of 0.32 alates per pot in the exclusion treatment and zero alates in the open treatment) were recorded in predator manipulation treatments after 14 days in both years.

In both years, generally low numbers of predators were found on open treatment potted plants (total = 104; n = 270 samples). Immature Chrysopidae were the most common predators, including eggs (0.17 ± 0.03 individuals/pot), hatched eggs (0.05 ± 0.02), and larvae (0.05 ± 0.01). Adults (0.05 ± 0.01) and nymphs (0.01 ± 0.01) of *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), and larvae (0.02 ± 0.01) and adults (0.01 ± 0.01) of Syrphidae were also observed. Very few predators were observed and removed from plants in predator exclusion cages: adults (0.06 ± 0.02) and nymphs (0.08 ± 0.03) of *O. insidiosus*, and larvae (0.01 ± 0.01) of Syrphidae.

Field populations of soybean aphids and their predators

Naturally occurring soybean aphid populations in the focal fields were low, but higher in 2014 (4.35 ± 0.74 aphids/plant, $n = 900$) than in 2013 (0.16 ± 0.06 aphids/plant, $n = 720$; $F_{1,25} = 16.95$, $p < 0.001$). A similar pattern was revealed by sweep-net sampling, with soybean aphid catches higher in 2014 (10.16 ± 2.42 aphids/25 sweeps, $n = 225$) than in 2013 (0.22 ± 0.12 aphids/25 sweeps, $n = 180$; $F_{1,25} = 20.63$, $p < 0.001$).

Sweep-net samples yielded 660 aphidophagous predators from six insect families, with an overall average of 1.63 ± 0.26 individuals/25 sweeps ($n=405$). Unless otherwise stated, for all analyses predators that are aphidophagous as adults and/or during their immature stages are included. For the adult stage, the most abundant predator family collected was Syrphidae (0.58 ± 0.16 ; 35.63% of the total capture), followed by Anthocoridae (0.55 ± 0.10 ; 33.97%), Chrysopidae (0.06 ± 0.02 ; 3.49%), Nabidae (0.03 ± 0.01 ; 1.82%), and Coccinellidae (0.02 ± 0.01 ; 1.06%). For predators in immature stages (i.e. larvae or nymphs, excluding eggs and pupae) the most abundant families collected were Anthocoridae (0.23 ± 0.05 ; 14.10%), followed by Syrphidae (0.07 ± 0.02 ; 4.32%), Nabidae (0.04 ± 0.01 ; 2.73%), Chrysopidae (0.03 ± 0.02 ; 2.12%), Hemerobiidae (0.01 ± 0.01 ; 0.61%), and Coccinellidae (0.002 ± 0.002 ; 0.15%) (Appendix III).

There were 88 aphidophagous predators recorded during visual plant counts from four families, with an overall average of 0.054 ± 0.01 individuals/plant ($n=1620$). The most abundant adult predator collected was Anthocoridae (0.018 ± 0.004 ; 32.95% of the total capture), followed by Syrphidae (0.006 ± 0.002 ; 10.23%), Chrysopidae (0.004 ± 0.002 ; 6.28%), and Coccinellidae (0.004 ± 0.002 ; 6.28%). For immature stages the most abundant family was Anthocoridae (0.014

± 0.003 ; 25.00%), followed by Syrphidae (0.009 ± 0.003 ; 17.05%), and Chrysopidae (0.001 ± 0.001 ; 1.14%) (Appendix III).

Predator movement between soybean and neighboring habitats

A total of 10,845 aphidophagous predators, from six insect families, were captured in the bi-directional Malaise traps deployed between soybean and neighboring habitats (Appendix III).

Since there was no difference between immigration (10.21 ± 2.08 individuals/trap/day) and emigration (15.61 ± 3.85 individuals/trap/day) when all predatory taxa were combined ($t = 1.56$, $df = 59$, $p = 0.12$), catches from both directions were pooled for analysis, resulting in an average catch of 12.91 ± 2.19 individuals/bottle/day. The three most numerous predator groups captured

were the same as those captured using sweep-nets, and were dominated by *Toxomerus marginatus* (Say) (Diptera: Syrphidae; 11.08 ± 2.01 individuals/bottle/day; 81.33% percentage of total capture), followed by *O. insidiosus* (0.26 ± 0.07 ; 1.92%); and *Chrysoperla carnea* (Stephens) and *Chrysopa* sp. (Neuroptera: Chrysopidae; 0.10 ± 0.01 ; 0.73%). Other predators included *Coccinella septempunctata* Linnaeus, *Harmonia axyridis* (Pallas), *Hippodamia tredecimpunctata* (Linnaeus), *H. variegata* (Goeze) and *Chilocorus* sp. (Coleoptera: Coccinellidae; 0.07 ± 0.01 ; 0.49%); Hemerobiidae (0.04 ± 0.01 ; 0.30%); and Nabidae (0.005 ± 0.002 ; 0.03%). *C. septempunctata* comprised the greatest percentage of lady beetles (38.80 %) and *C. carnea* of aphidophagous green lacewings (60.63 %).

Association of landscape complexity with aphid suppression

In this study, 3,944 land-cover areas (i.e. total polygons in Appendix II) were quantified digitally in 27 landscapes. The studied landscapes represented a gradient of complexity, ranging from areas dominated by agriculture to those with moderate proportions of natural and riparian

vegetation, with Simpson's diversity index values ranging from 0.49 to 0.90. Five field crops were the dominant land-cover types at the spatial scale of 2 km: soybean (24.9 % of the total area, range 6.9 – 48.4 %), cereals (19.8 %, 2.9 – 46.9 %), canola (13.2 %, 0.0 – 36.2 %), corn (10.8 %, 0.0 – 36.2 %) and alfalfa (7.2 %, 0.0 – 34.6%). Grass forage crops (*Bromus* spp.; Canary grass, *Phalaris canariensis* L.; and other green grass patches) accounted for 1.8 % (0.0 – 9.9 %). All other crops combined represented 1.5 % (0.0 – 14.7 %) of the landscapes. For non-crop areas, woodland (6.3 %, 0.3 – 40.3 %), riparian vegetation (2.8 %, 0 – 11.8 %), field border grass (2.3 %, 0.6 – 5.0 %), pasture (1.4 %, 0 – 7.0%) and shrubland (0.8 %, 0 – 4.9 %) were the most important land-cover types (see Appendix II). Marshes (0.6 %), University research plots (0.3 %), and fallow fields (0.1 %) represented smaller areas of the landscapes and were excluded from the multiple regression analysis.

In all significant multiple regression models, aphid potential growth, estimated using the predator exclusion treatment, was positively associated with the final aphid population size in the open treatment and the highest partial correlation coefficient (0.56 – 0.77; Table 2, Figure 3a, 4a, and 5a; see Appendix IV). There were only three landscape models with substantial support from the data (i.e. with $\Delta i < 2$), out of 13 significant landscape models (Table 2; see Appendix IV, for all significant models). The best landscape model was observed at the spatial scale of 2 km and showed that final aphid population size in the open treatment had a negative association with the proportion of cereals (Figure 3b) and a weak positive association with the proportion of canola (Figure 3c) in the landscape. These associations were consistent in all other significant landscape models at various spatial scales (Appendix IV). Landscape models with similar explanatory power revealed a positive association between final aphid population size in the open treatment with the proportion of woodland at the spatial scale of 0.5 km and a negative association with the

proportion of cereal crops at the spatial scale of 1.5 km (Table 2). Finally, no significant relationships were found between final aphid population size in the open treatment and habitat diversity, richness or evenness (included in separate alternative models with other landscape variables to avoid collinearity).

Association of predator movement with aphid suppression

Models relating movement of predators with aphid suppression had lower AIC_c values and slightly higher explanatory power than models with landscape variables only (Table 2). The best supported model indicated that final aphid population size in the open treatment was negatively associated with aphidophagous green lacewings and positively associated with brown lacewings (Figures 4b and 4c). Another model with high explanatory power ($Adj. r^2 = 0.55$) but less support from the data ($AIC_c = 68.06$) suggested that higher levels of lady beetle movement were negatively associated with final aphid population size in the open treatment (partial correlation = -0.37 , $p = 0.00002$; see Appendix IV).

Combined associations of predator movement and landscape complexity with aphid suppression

Combining landscape and predator movement variables yielded models with more support than models with landscape variables alone, but with slightly less support than models with predator movement variables alone. Twelve significant models were fitted and five models had substantial support at all five spatial scales (Table 2; see Appendix IV for all significant models). The model with the highest support suggests that final aphid population size in the open treatment was negatively associated with green lacewings and positively associated with canola and field border grass at the spatial scale of 0.5 km (Table 2, Figure 5). These relationships were consistent at other spatial scales (Table 2). Final aphid population size in the open treatment was

negatively associated with the movement of lady beetles and the proportion of cereals at the spatial scale of 2 km (Table 2) and these relationships were also consistent with other significant models at lower spatial scales (Appendix IV). Consistent with predator movement models, movement of brown lacewings had a positive relationship with final aphid population size in the open treatment in all models (Table 2 and Appendix IV). Finally, movement of green lacewings and proportion of shrubland at the 1.5 km radius spatial scale were negatively associated with final aphid population size in the open treatment (Table 2).

Several predator movement and landscape variables were not combined in the same models due to correlation. For example, movement of green lacewings was positively associated with the proportion of cereals in the landscape at the spatial scale of 2 km (Pearson's correlation $r = 0.43$, $df = 25$, $p < 0.02$; Appendix V). Similarly, movement of brown lacewings had a positive association with the proportion of canola at the spatial scale of 1.5 km ($r = 0.40$, $df = 25$, $p < 0.05$; Appendix V), and with the proportion of field border grass at the spatial scales of 1.5 km ($r = 0.63$, $df = 25$, $p < 0.001$) and 2 km ($r = 0.48$, $df = 25$, $p < 0.05$).

There was no evidence of spatial autocorrelation in the best landscape model (Moran's $I = -0.25$, $p = 0.11$), and in the best model combining landscape and predator movement variable (Moran's $I = -0.14$, $p = 0.45$). However, there was spatial autocorrelation in the most supported predator model (i.e. combining movement of green and brown lacewings; Moran's $I = 0.28$, $p = 0.02$). Inspection of partial residual plots revealed no evident patterns of association between the movement of green and brown lacewings and field locations for any models with these variables, including the most supported predator model. There was no evidence of spatial autocorrelation in any other model with movement of green lacewings and brown lacewings (all $p > 0.13$). Based

on these analyses, there was no adjustment for spatial autocorrelation in the multiple regression analyses presented here.

Discussion

Previous studies have shown significant associations between landscape complexity, predator abundance and diversity, and pest suppression (e.g. Bianchi et al. 2006; Chaplin-Kramer et al. 2011). Although these associations are likely mediated through the interchange of predators between crops and other habitats at the landscape scale (Tscharntke et al. 2007; Schellhorn et al. 2014), the importance of this mechanism has not been explicitly tested. In this study, I show for the first time a direct association between pest suppression and patterns of predator movement between crops and neighboring habitats in the agricultural landscape. Furthermore, I demonstrate that predator movement variables have similar or even more explanatory power than traditional landscape variables to predict pest suppression.

Soybean aphid suppression by generalist predators

This study demonstrates, for the first time, widespread suppression of soybean aphid by generalist predators in Manitoba, supporting previous results found in other soybean growing areas in North America (e.g. Costamagna et al. 2007; Gardiner et al. 2009a; Woltz et al. 2012) and confirming the role of generalist predators in reducing rates of population growth of generalist pests (Symondson et al. 2002). In this study, the final soybean aphid population size in the exclusion treatment was 3.8 times greater than the aphids in the open treatment after two weeks. Costamagna and Landis (2006) found final soybean aphid population size in predator exclusion cages four to seven times higher than open and sham cage treatments in Michigan. Similarly, a study in Indiana showed that final soybean aphid population size was 0 – 5.6 times

greater in the absence of predators compared to plants where predators had access (Desneux et al. 2006) and Gardiner et al. (2009a) found 5.3 times greater number of soybean aphids on plants in the predator exclusion treatment compared to open plants, after two weeks, in Iowa, Michigan, Minnesota, and Wisconsin. The level of soybean aphid suppression observed in my study is well within the range observed in other North American studies, and demonstrates the presence of an effective assemblage of predators in Manitoba.

Predator exclusion and open treatments varied in several factors that may also have influenced final aphid population size, including restrictions on aphids and predator movement, and microclimate conditions. To minimize apterous aphids walking from plants in the open treatment, I removed any adjacent soybean plants touching the treatment plants (Costamagna et al. 2013). Nearby field plants inspected revealed no aphids, suggesting that sentinel aphids did not leave the open treatment. In addition, there was a negligible number of alates recorded in the predator exclusion treatment. These results suggest that confinement within the predator exclusion treatment did not artificially inflate aphid populations. Large differences between treatments suggest that the low numbers of immature predators (*O. insidiosus* and hover fly larvae) found inside the exclusion cages had also minimal effects on aphid population size. Although microclimatic conditions were likely slightly different between open and predator manipulation treatments (they were not monitored in our study), previous studies have shown that differences are minimal and do not affect the levels of soybean aphid suppression attributed to predators. This was demonstrated by the similar final aphid population sizes obtained between open and sham cage treatments (i.e. similar to predator exclusion cages, but with openings that allow predator access to aphids) in several separate studies in Michigan (Fox et al. 2004; Costamagna and Landis 2006; Costamagna et al. 2007; Costamagna et al. 2008; Costamagna and

Landis 2011). There were moderate rainfall events near two fields in 2013 (31.8 mm/24 h, 25th July) and one field in 2014 (22.4 mm/24 h, 4th August) in Gimli (Government of Canada 2017). However, final aphid population size in the open treatment on the fields affected was well within the range of the other fields (2013: 11.8 ± 5.7 versus 17.3 ± 8.2 ; 2014: 93.8 versus 113.0 ± 88.0 ; mean aphids/pot \pm SD, rainy versus ‘normal’ fields, respectively), suggesting that rainfall was not a major mortality factor in the open treatment. In summary, most of the reduction in final aphid population size observed in the open treatment was likely due to mortality caused by predators.

The assemblage of generalist predators observed in Manitoba differed from other assemblages found suppressing soybean aphid in other regions of North America. In Manitoba, hover flies (Syrphidae) were the most common generalist predators recorded in bi-directional Malaise traps and sweep-net samples, followed by adult minute pirate bugs (*O. insidiosus*), and aphidophagous green lacewings (Chrysopidae). This could indicate higher rates of movements across fields for hover flies than for minute pirate bugs. Soybean aphid populations were extremely low during both years of study, which may also result in a different assemblage of predators colonizing soybeans compared to other regions where aphid populations are more consistently found. For example, lady beetles are the dominant predator in natural enemy assemblages in soybean in Québec (Mignault et al. 2006), Iowa (Cox et al. 2014), Minnesota (Bannerman et al. 2015) and Michigan (Costamagna et al. 2007). Alternatively, studies in Iowa, Michigan, Minnesota, Nebraska, and Wisconsin show that minute pirate bugs are the most common predators found in soybean fields in some regions (Brosius et al. 2007; Costamagna and Landis 2007; Noma et al. 2010). My results, combined with others, suggest that generalist predators may have complementary roles in aphid suppression, resulting in assemblages with

very different species composition achieving similarly high levels of aphid suppression in different regions.

Association of landscape complexity with aphid suppression

The proportion of cereals (wheat, oat, and barley combined) showed a consistent negative association with number of soybean aphids in the open treatment at multiple scales. In Wisconsin, Stack Whitney et al. (2016) found that unmanipulated soybean aphid abundance is negatively correlated with several minor agricultural crops, including small grains, alfalfa and beans. Most cereals are seeded in late April to early May in Manitoba (Gavloski and Meers 2011), providing habitat for aphids early in the season. Several aphid species, including the English grain aphid *Sitobion (Macrosiphum) avenae* Fabricius, the bird cherry-oat aphid *Rhopalosiphum padi* (Linnaeus), and the greenbug *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae) colonize cereal fields from June to August in Manitoba, and only rarely require insecticide applications for control (Bakker 1974; Gavloski and Meers 2011; Gavloski 2015a), (Malyk and Robinson 1971; Bakker 1974; Bakker and Robinson 1975; Gavloski and Meers 2011; Gavloski 2015a). These aphid populations are likely to support predators, and previous studies report several aphidophagous natural enemies associated with cereal crops in Manitoba, including lady beetles, green lacewings, brown lacewings, and parasitoids (Bakker 1974; Gavloski and Meers 2011). By mid to late July, wheat fields are near physiological maturity (Manitoba Agriculture 2017a), and decrease in suitability for aphid populations, suggesting that predators may need to move to other habitats to find prey. The positive correlation between the proportion of cereals in the landscape and the movement of green lacewings further suggests that cereals can act as sources of beneficial insects for soybean. Altogether, these findings suggest

that landscapes with high proportion of cereals may support populations of aphidophagous predators that spill into other crops, including soybean.

In this study, a higher proportion of canola in the landscape was associated with a higher final soybean aphid population size in the open treatment. Several aphid species are commonly observed in canola in Manitoba, such as the green peach aphid, *Myzus persicae* (Sulzer), the turnip aphid, *Lipaphis pseudobrassicae* (Davis) and the cabbage aphid, *Brevicoryne brassicae* (Linnaeus) (Gavloski et al. 2011). Among them, green peach aphids move into canola early in the season, as they prefer canola seedlings, and cabbage aphids congregate on flowers (Gavloski et al. 2011) in late July (K.G.L.I.S., personal observation). Lady beetles, green lacewings, hover flies, and parasitoids move into canola fields to feed on aphids throughout the growing season (Gavloski et al. 2011). Predators may also migrate into canola to feed on nectar and pollen during the flowering period (McEwen et al. 2007; Hodek et al. 2012), which was coincident with my experiments. Therefore, canola and soybean would typically have aphid populations developing at similar times, suggesting that both crops may compete for predators. Furthermore, these results provide empirical support to the hypothesis that temporal relationships between different habitats may be important to fully understand predator-pest dynamics in agricultural landscapes (Schellhorn et al. 2014).

In contrast with previous studies (e.g. Thies and Tschardtke 1999; Rusch et al. 2016), total non-crop area (i.e. combining woodland, and other semi-natural vegetation categories) was not associated with aphid suppression. While the proportion of shrubland was negatively associated with final aphid population size in the open treatment at the spatial scale of 1.5 km, this cover represents on average less than 1% of the landscape (Appendix II). In contrast, the proportion of woodland land-cover types (trees, hedgerows and forested areas) had positive and

consistent associations with number of soybean aphids in the open treatment at multiple scales, particularly at the spatial scale of 0.5 km. Predators in non-crop areas have access to alternative prey, shelter, moderated temperatures, and overwintering sites, among other resources that are limited in most field crops early in the season and after crop maturity and harvesting (Landis et al. 2000; Sutherland et al. 2001; Bianchi et al. 2006). Most previous studies were conducted in areas where soybean aphids are usually present at moderate to high levels in soybean (Gardiner et al. 2009a; Woltz and Landis 2013; Mitchell et al. 2014; Maisonhaute et al. 2017). In Manitoba, naturally occurring soybean aphids were negligible during both years of study. It is therefore possible that woodland habitats were more attractive to predators due to the lack of sufficient prey in soybean fields, decreasing predation on sentinel aphids. Results from the bi-directional malaise trap sampling do not support this hypothesis. Hover fly movement from woodlands to soybean was significantly higher than in the opposite direction, and the same trend was found for aphidophagous green lacewings, minute pirate bugs, lady beetles and brown lacewings (see results in Chapter 4), suggesting that woodland can actually be a source of predators to soybean. Alternatively, woodland habitats in Manitoba may lack resources present in similar habitats from other regions, thus supporting lower predator populations. The overall low abundance of predators in woodland borders compared to wheat, grass and, for lady beetles, alfalfa borders (see results in Chapter 4), provide support for this hypothesis. More research is needed to determine the role of woodland habitat as source of predators in Manitoba, when resources for predators are scarce in crops.

Agricultural landscapes in Manitoba differ in composition when compared to other regions of North America, providing an alternative explanation for the discrepancy between this study and others on the role of woodland areas in soybean aphid suppression. Previous studies

were conducted in landscapes dominated by corn and soybean (Gardiner et al. 2009a; Noma et al. 2010; Mitchell et al. 2014; Maisonhaute et al. 2017) whereas agricultural landscapes in Manitoba had high proportions of cereals and canola, perhaps altering the dynamics of predators in woodlands. A recent study also found higher soybean aphid abundance associated with a greater proportion of forest in Wisconsin, possibly due to the presence of overwintering hosts, buckthorn (*Rhamnus* spp.), in forests (Stack Whitney et al. 2016). In Manitoba, the lack of overwintering populations may result in a lack of correlation between the abundance of soybean aphids and the distribution buckthorn (Gavloski 2006; Gavloski 2008). A study on predation on melon aphid, *A. gossypii*, in horticultural landscapes in Australia showed negative associations between proportion of natural vegetation in the landscape and aphid suppression, also most likely due to low levels of alternative resources present in natural vegetation (Costamagna et al. 2015). The relationship among proportion of woodland in particular, and non-crop areas in general, predators and pest suppression needs to be further studied before generalizations can be made.

Association of predator movement with aphid suppression

In this study, the pattern of movement of key predators was only a slightly better predictor of soybean aphid suppression than landscape variables alone, providing some support for my initial prediction. This result suggests that patterns of predator movement are closer to the “realized” contribution of the landscape to pest suppression, contrasting with the “potential” contribution of the landscape estimated earlier with landscape complexity measures. Several factors may contribute to a potential mismatch between levels of pest control services and conventional measures of landscape complexity, including variability in crop management practices among farms (particularly pesticide use), and variability in bottom-up resources across patches with the

same land-cover type. This in turn results in variable levels of resources for predators within the same land-cover type in the landscape that may make it difficult to elucidate how landscape patterns influence pests (Chaplin-Kramer et al. 2011). Timing of predator arrival has also been shown to potentially confound landscape effects on pest suppression (Costamagna et al. 2015), further suggesting that actual patterns of predator movement would more accurately predict pest suppression than measures of landscape complexity.

Captures of green lacewings in bi-directional Malaise traps were negatively associated with final aphid population size in the open treatment. Green lacewings are normally associated with non-crop areas before the start of the growing season (Tauber et al. 1993; Bianchi et al. 2006) and they can complete several generations during the summer, following aphid populations on various crops (Tauber et al. 1993; McEwen et al. 2007). There was also a weak negative association between movement of lady beetles and final aphid population size in the open treatment. The lack of strong associations between movement of lady beetles and aphid suppression may be due to the low numbers of lady beetles captured by bi-directional Malaise traps, which reduces the power to detect significant associations, and by the correlation between movement of lady beetles and green lacewings, which prevented the inclusion of both variables in the same model. These results suggest that movements of green lacewings and lady beetles across the landscape represent the realized contribution of the landscape to aphid suppression in soybeans.

Brown lacewings were present in low numbers, but showed a positive relationship with final aphid population size in the open treatment, the opposite to the pattern observed for movement of green lacewings and lady beetles. There were no records of brown lacewings in the open treatment or in visual plant counts, but a few larvae were collected in sweep-net samples.

The number of brown lacewings increased with the proportion of canola and field border grass in the landscape, which also had positive associations with number of soybean aphids in the open treatment. This suggests canola and field border grass areas may act as sources of brown lacewings, and therefore the positive relationship between brown lacewings and soybean aphids may be due to a correlation between brown lacewings and the proportion of canola in the landscape.

The most common aphidophagous predator captured from late July to early August in the bi-directional Malaise trap samples was the hover fly *T. marginatus*. Similarly, Eckberg et al. (2015) found that *T. marginatus* was the most abundant species recorded from July to August in Minnesota, USA. Despite the abundance of *T. marginatus*, this predator was not associated with final aphid population size in any of the multiple regression models. Several factors may affect the effectiveness of this predator on soybean aphid populations. Noma and Brewer (2008) demonstrated that hover fly abundance was lower in larger soybean plots (0.5 – 1.0 ha) compared to the small soybean plots (0.01– 0.02 ha). Hover fly eggs and larvae were recorded in very low numbers in the large soybean fields used in my study (in average 72 ha), suggesting that hover flies may not be effective in finding sentinel aphid colonies in large fields. Another potential limiting factor in the effectiveness of hover fly larvae to control aphids could be intraguild predation caused by other generalist predators, such as lady beetles (*H. axyridis* and *C. septempunctata*) and green lacewings (*Chrysoperla* sp.), as shown for other hover fly species (Hindayana et al. 2001; Ingels and De Clercq 2011). Finally, Verheggen et al. (2009) demonstrated that pubescence on soybean plants reduces the movement and performance of hover fly larvae and results in low deposition of eggs on soybean. More studies are needed to

elucidate the causes of a lack of association between aphid suppression and the abundance of hover flies.

Combined associations of predator movement and landscape complexity with aphid suppression

Combining both landscape and predator movement variables resulted in models with more explanatory power than landscape variables alone. Interestingly in my study, the two models with the most support combined movement of green lacewings with landscape variables at the two smallest spatial scales measured (i.e. spatial scales of 0.25 km and 0.5 km). This result may be the consequence of excluding the proportion of cereals from the initial models combining the two types of variables, as the proportion of cereals was highly correlated with the movement of green lacewings. This also suggests that the movement of green lacewings is a better predictor of soybean aphid suppression than the proportion of cereal crops, further supporting my initial expectation of more precise predictions based on predator movement than on landscape variables. Furthermore, it suggests that accounting for the movement of the main predators in the system can reveal the role of other land-cover types in the landscape, which may not be significant when using landscape variables alone.

Proportions of field border grass and canola were the best landscape predictors in combined models, having negative associations with soybean aphid suppression. Previous studies suggest that predators may prefer to stay within grassy field borders at times when pest abundances within field crops are low (e.g. Hodek et al. 2012). However, Altieri and Letourneau (1982) suggested that cutting field border grass regularly during the crop-growing season will likely encourage predators to move to neighboring field crops. In my study, I did not record

information about cutting dates for field border grass patches around studied fields and surrounding landscapes. Further experiments focusing on determining the population dynamics of predators in field border grass are needed to fully understand the role that these habitats perform at the landscape scale.

A few studies have tested the combined association of natural enemies and landscape variables with pest suppression and crop damage. Bengtsson (2015) found that barley yield is more related to the intensity of farming practices than with biological control of aphids or landscape complexity variables in Sweden. In contrast, Maisonhaute et al. (2017) found that natural enemy abundance, alone or combined with landscape variables, explains cumulative abundance of soybean aphid in Québec. Grez et al. (2014) observed that when lady beetles and hover flies are abundant, they have significant associations with aphid suppression in alfalfa, but when their abundance is low, then landscape composition is the best predictor of aphid suppression. However, these previous studies measured the association between pest suppression and predators present in the field, thus confounding the contribution of predator populations established in the field and predators migrating from extra-field habitats.

My study contributes the first empirical evidence demonstrating an association between pest suppression and patterns of predator movement between crops and neighboring habitats at the landscape scale, providing a mechanistic link between landscape complexity and ecosystem functioning. This study demonstrates that models of pest suppression incorporating patterns of predator movement have similar or even more explanatory power than models with only traditional landscape complexity variables. I found that different crops and semi-natural land covers have distinct associations with pest suppression at the landscape scale, suggesting that grouping land-cover types into large categories (e.g. crop versus non-crop area) may not be

appropriate for all systems or regions. Finally, this study suggests that quantification of predator movement into field crops may help to determine the most important species of predators that provide pest control services in a particular habitat and the habitats that can act as their sources at the landscape scale, information that can be incorporated into the design of agricultural landscapes that maximize pest control services by natural enemies.

Table 1. Results of the ANOVA for effects of field, predator manipulation treatments and week on final soybean aphid population size after two weeks of manipulation in 27 soybean fields in Manitoba, in 2013 and 2014.

Factor	Sum of squares	<i>df</i>	Mean square	<i>F</i>-Value	<i>p</i>-Value
Field	239.76	26	9.22	11.89	< 0.0001
Predator manipulation	313.26	1	313.26	403.98	< 0.0001
Field × predator manipulation	61.01	26	2.35	3.03	< 0.0001
Between subjects	167.49	216	0.78		
Week	156.16	1	156.16	681.72	< 0.0001
Field × week	46.48	26	1.79	7.81	< 0.0001
Predator manipulation × week	6.01	1	6.01	26.24	< 0.0001
Field × predator manipulation × week	9.06	26	0.35	1.52	0.057
Within subjects	49.48	216	0.23		

Table 2. Summary statistics of multiple regression models assessing the relationship between final population size of soybean aphids exposed to predation in the open treatment and landscape variables (landscape models), levels of aphidophagous predator movement in field borders (predator models), and both sets of variables combined (landscape + predator models) at different spatial scales in Manitoba

Scale (km)	Models	Log-likelihood	AIC _c	Δi	w_i	Adj. r^2	P value	Partial correlation with dependent variable
Null model								
	I + A	-30.69	68.43	4.37	0.03	0.52	< 0.0001	
Landscape models								
2	I + A*** - CE* + CA	-25.60	64.06	0.00	0.29	0.64	< 0.0001	A (0.65), CE (-0.40), CA (0.05); Moran's $I = -0.25, p = 0.11$
0.5	I + A*** + W* + CA**	-26.06	64.97	0.91	0.18	0.63	< 0.0001	A (0.56), W (0.43), CA (0.48)
1.5	I + A*** - CE*	-27.84	65.49	1.43	0.14	0.59	< 0.0001	A (0.67), CE (-0.38)
Predator models								
	I + A*** - gl** + bl	-24.99	62.83	0.00	0.64	0.66	< 0.0001	A (0.68), gl (-0.52), bl (0.26); Moran's $I = 0.28, p = 0.02$
	I + A*** - gl**	-27.22	64.26	1.43	0.31	0.61	< 0.0001	A (0.74), gl (-0.51)
Landscape + predator models								
0.5	I + A*** - gl** + CA+ BG**	-23.57	63.34	0.00	0.24	0.68	< 0.0001	A (0.77), gl (-0.52), CA (0.34), BG (0.18); Moran's $I = -0.14, p = 0.45$
0.25	I + A*** - gl** + CA* + BG	-23.98	64.17	0.83	0.16	0.67	< 0.0001	A (0.76), gl (-0.54), CA (0.39), BG (0.10)

Scale (km)	Models	Log-likelihood	AIC _c	Δi	w_i	Adj. r^2	P value	Partial correlation with dependent variable
1.5	I + A*** - gl*** - SH*	-25.66	64.19	0.85	0.15	0.64	< 0.0001	A (0.73), gl (-0.58), SH (-0.38)
1	I + A*** - gl** + CA	-25.84	64.54	1.20	0.13	0.63	< 0.0001	A (0.73), gl (-0.50), CA (0.25)
2	I + A*** - co - CE* + bl	-24.44	65.08	1.74	0.10	0.65	< 0.0001	A (0.73), co (-0.37), CE (-0.46), bl (0.17)

Notes: Model terms include intercept (I); aphid potential growth estimated using final aphid population size in exclusion cages (A); landscape variables: total proportion of field border grass (BG), cereals (CE), canola (CA), woodland (W), soybean (SB), shrubland (SH); and predator movement variables: average daily catch in bi-directional Malaise traps of aphidophagous green lacewings (gl), brown lacewings (bl) and lady beetles (co) during two weeks. Adjusted (Adj.) r^2 is shown. In all models, the natural log of the average final aphid population size in the open treatment in each field was the dependent variable. For each type of model, the model presented first and in bold was the most supported by the data (smallest AIC_c); also shown are competing models with substantial support in each of the three model groups ($\Delta i < 2$). Akaike weight (w_i) indicates the support of each model within a group of models. Tests of autocorrelation for the residuals for the three most supported models are shown using Moran's I statistics. (* P<0.05; ** P<0.01; *** P<0.001)

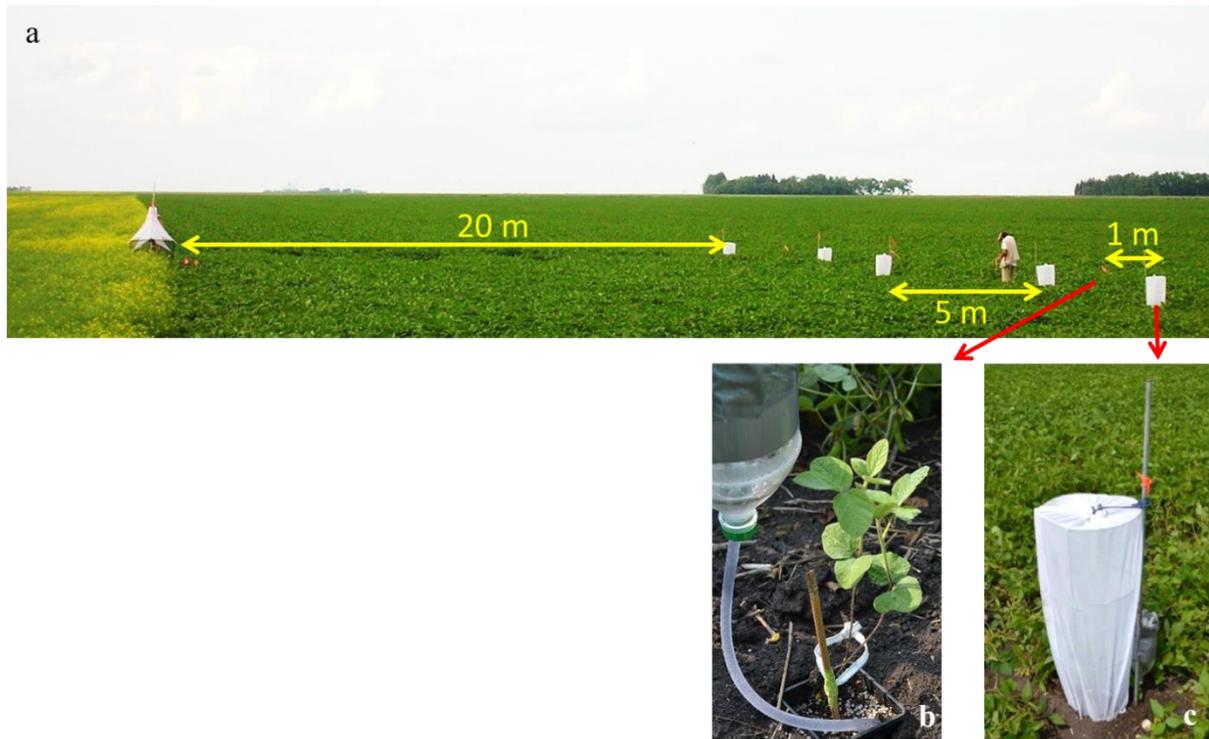


Figure 1. Experimental layout in a soybean field. a) Ten pots with soybean plants (two plants per pot) established 20 m from the field border, and bi-directional Malaise traps established at the soybean-canola field border. b) Open and c) predator manipulation treatments arranged in pairs separated by approximately 1 m, whereas the distance between pairs of experimental plot was 5 m.

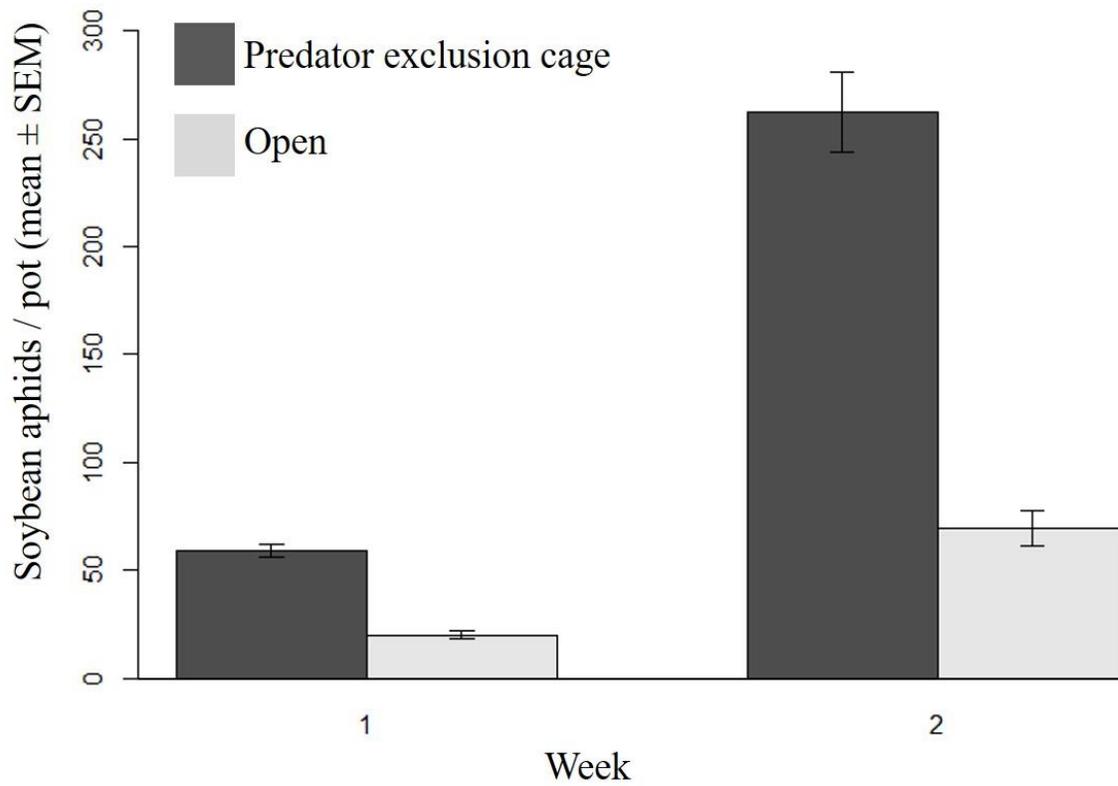


Figure 2. Number of soybean aphids, *A. glycines*, per pot (mean \pm SEM) present in predator manipulation and open treatments; 1 and 2 weeks after manipulation. Experiments were conducted in 27 soybean fields in Manitoba during 2013 and 2014.

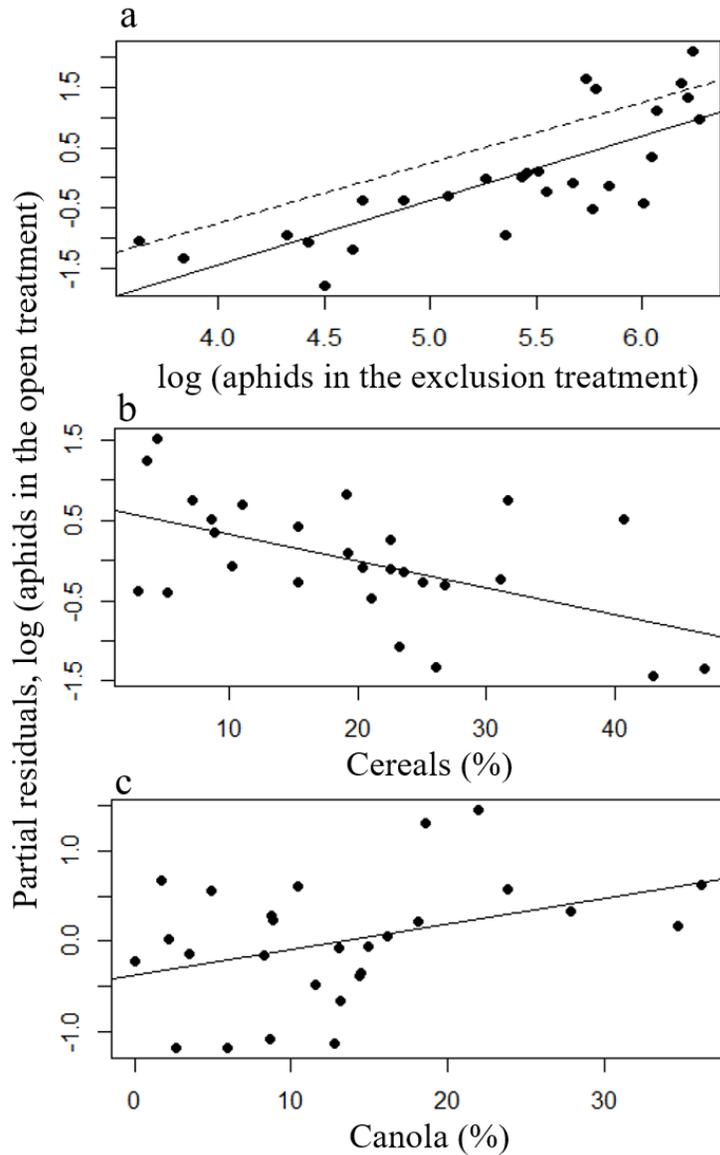


Figure 3. Associations between final soybean aphid population size (ln aphids/pot) in the open treatment after two weeks exposed to predation (represented by the partial residuals of the model when controlled for other variables in the model) and (a) final aphid population size in the predator exclusion treatment (used as control for different environmental conditions among fields and years; the dashed line has a slope = 1 and is shown for reference), proportion of the landscape with (b) cereals and (c) canola, at a spatial scale of 2 km. See Table 2 for model

statistics. Each point represents a landscape ($n = 27$) and is the average of five sentinel aphid colonies.

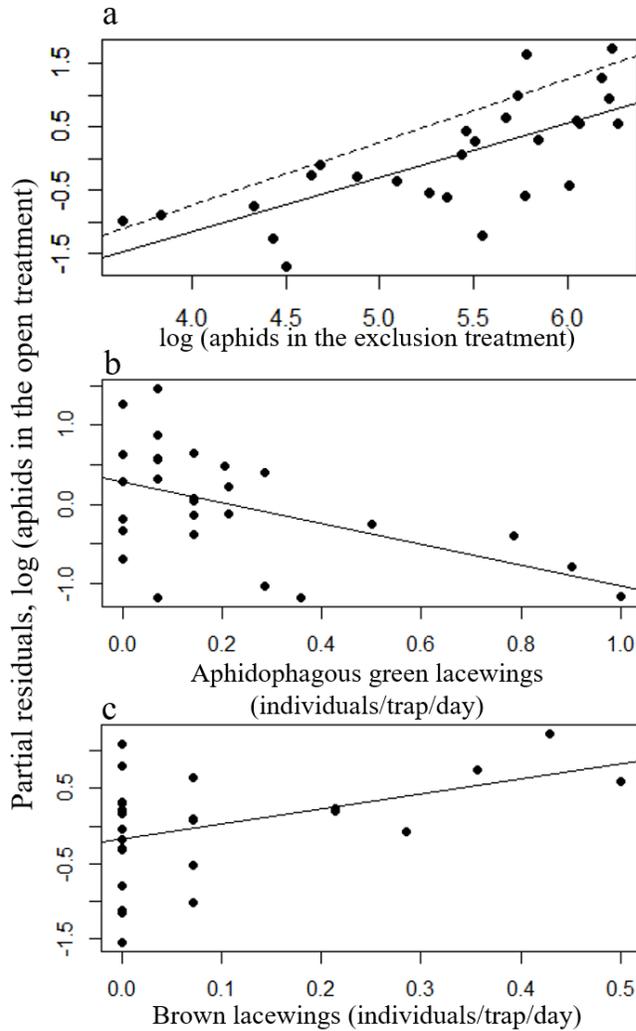


Figure 4. Associations between final soybean aphid population size (\ln aphids/pot) in the open treatment after two weeks exposed to predation (represented by the partial residuals of the model when controlled for other variables in the model) and (a) final aphid population size in the predator exclusion treatment (used as control for different environmental conditions among fields and years; the dashed line has a slope = 1 and is shown for reference), and movement (individuals/trap/day) of (b) aphidophagous green lacewings (*C. carnea* and *Chrysopa* sp.) and (c) brown lacewings. See Table 2 for model statistics. In (b) and (c), each point represents average predator capture in bi-directional Malaise traps per field.

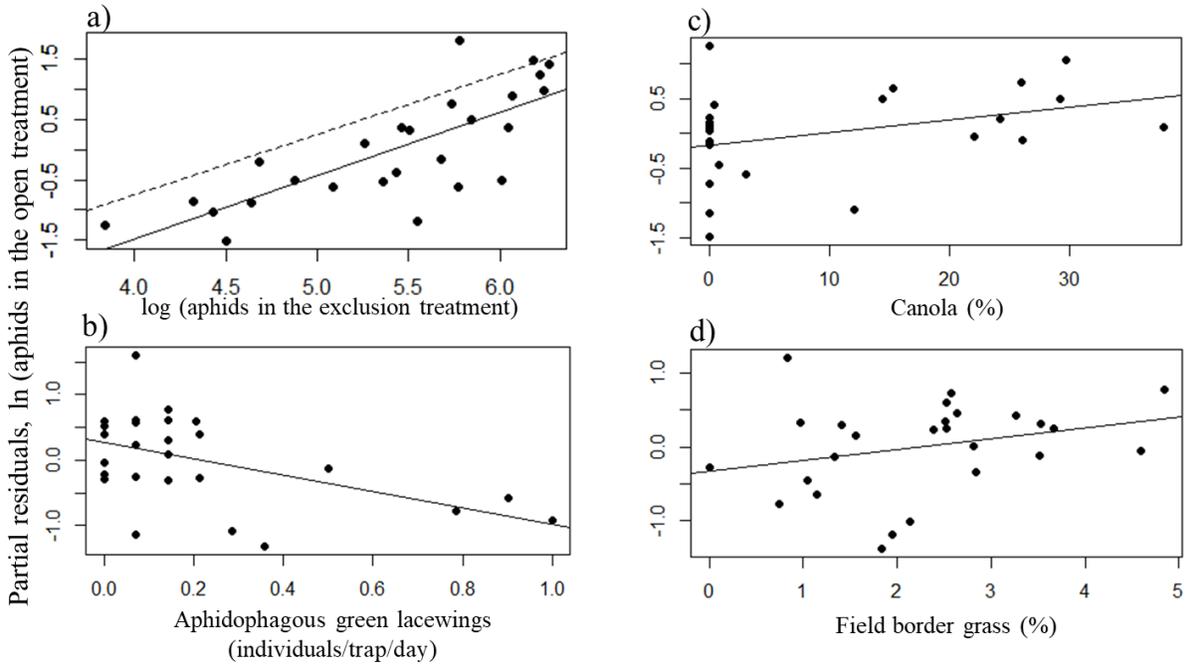


Figure 5. Associations between final soybean aphid population size (log aphids/pot) in the open treatment after two weeks exposed to predation (represented by the partial residuals of the model when controlled for other variables in the model) and (a) final aphid population size in the predator exclusion treatment (used as control for different environmental conditions among fields and years; the dashed line has a slope = 1 and is shown for reference) and movement of (b) aphidophagous green lacewings (*C. carnea* and *Chrysopa* sp.) (individuals/trap/day), proportion of the landscape in (c) canola and (d) field border grass, within a spatial scale of 0.5 km of the predator manipulation experiment. See Table 2 for model statistics and Figure 2 and 3 for explanation of variables. In (b), each point represents average predator capture in bi-directional Malaise traps per field.

CHAPTER 4: ARE ADJACENT HABITATS CONTRIBUTING APHIDOPHAGOUS PREDATORS TO SOYBEANS?

Abstracts

Generalist predators have been shown to strongly suppress soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) populations in North America. The role of adjacent habitats as sources of aphidophagous predators has not been studied directly however. Here, movement of aphidophagous predators was quantified between soybean and adjacent habitats common in Manitoba, such as alfalfa, canola, wheat, border-grass and woodland using 14 bi-directional Malaise traps (BMT) during 2013 (three weeks) and 16 BMT during 2014 (4 weeks). Movement between soybean and alfalfa fields was also studied in two mark-release-recapture experiments using seven-spotted lady beetles, *Coccinella septempunctata* (Linnaeus) (Coleoptera: Coccinellidae), characterizing displacement, within and between crops. The most abundant predators moving between soybean and adjacent fields were hover flies (Diptera: Syrphidae). The identity of the adjacent habitat affected the net movement of predators to soybean. Captures of hover flies were higher from woodlands to soybean than vice versa, and a similar trend was found for lady beetles, minute pirate bugs, green and brown lacewings. In contrast, greater numbers of hover flies and green lacewings moved from soybean to canola. Lady beetles showed higher immigration to than emigration from soybean, when movement from all adjacent habitats was combined. In a high lady beetle abundance year, overall movement of lady beetles was higher in alfalfa, wheat and grass borders but did not differ in a low abundance year. Mark-release-recapture experiments showed a trend of *C. septempunctata* moving in higher numbers, and over longer displacement distances from soybean to alfalfa than vice versa, probably due to a lack of naturally occurring aphids in soybean. Altogether, these results show that type of adjacent habitat and predator identity affect the directionality of predator movement to soybean. This

information should be considered when designing agricultural landscapes to maximize benefits from predators moving between adjacent habitats.

Introduction

Increased habitat fragmentation in agricultural landscapes is a common consequence of agricultural intensification and is associated with loss of biological diversity, loss of natural enemies, and reductions in the biological control of pests (e.g. Kruess and Tscharrntke 1994; Tscharrntke et al. 2005). Habitat fragmentation increases the number of borders between crops and non-crop habitats in agricultural landscapes (Rand et al. 2006). Predators move across these field borders, and cyclic colonization of crops from extra-field habitats is important for pest regulation (Wissinger 1997). In addition to habitat fragmentation, several land management practices, including cultivation, use of fertilizers and pesticides, and harvesting create disturbances in crops that negatively affect predators and their biological control capabilities (Östman et al. 2001; Bianchi et al. 2006; Schellhorn et al. 2014). Therefore, most predators rely at least during part of their life cycle on non-crop habitats to obtain food, mates, and reproductive sites (Landis et al. 2000).

The directionality of predator movement (i.e. net immigration or emigration from a field border) across habitat boundaries is influenced by adjacent habitats and although it can be assessed using several methods (Southwood and Henderson 2009), relatively few studies have quantified insect movement between adjacent habitats in agricultural landscapes (Lewis 1969; Duelli et al. 1990; Macfadyen and Muller 2013; Macfadyen et al. 2015; González et al. 2016). For example, Duelli et al. (1990) found using directional sticky cards in northwestern Switzerland that corn fields have higher emigration of lady beetles to adjacent barley and wheat fields. Using directional pitfall traps, the same study show higher immigration of carabid beetles

in corn from wheat and barley borders (Duelli et al. 1990). Macfadyen and Muller (2013) and Macfadyen et al. (2015) conducted studies using bi-directional Malaise traps, and found differences in insect community composition (i.e. predators, parasitoids and herbivores) and in movement patterns of insects in canola and cereals (wheat/barley) associated with different adjacent habitats in Australia.

Soybean, *Glycine max* (L.) Merr. (Fabales: Fabaceae), is a globally important crop that is a good source of protein for human diets, and is also used for livestock feeds, oil, and biofuel production (Masuda and Goldsmith 2009). The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is an important soybean pest that reduces soybean yields significantly (Wu et al. 2004; Heimpel et al. 2010; Ragsdale et al. 2011). Since its arrival in North America in 2000, soybean aphid spread to 30 states and three Canadian provinces by 2009 (Ragsdale et al. 2011), and soybean scouting services have increased 40-fold and insecticide applications increased 130-fold (Tilmon et al. 2011). Several studies have shown that aphidophagous predators, including different species of lady beetles (Coleoptera: Coccinellidae), minute pirate bugs (Hemiptera: Anthocoridae), damsel bugs (Hemiptera: Nabidae), and larvae of hover flies (Diptera: Syrphidae) and lacewings (Neuroptera: Chrysopidae and Hemerobidae) are able to suppress soybean aphid populations in North America (Costamagna and Landis 2006; Desneux et al. 2006; Costamagna et al. 2007; Costamagna et al. 2008; Ragsdale et al. 2011).

Landscape complexity is associated with predator abundance and efficacy on soybean aphid suppression in soybean fields (Gardiner et al. 2009a; Woltz et al. 2012). Gardiner et al. (2009a) found that higher landscape complexity increases suppression of soybean aphid and lady beetle abundance. In contrast, a recent study in Québec has shown that abundance of soybean aphid was higher in soybean fields in complex landscapes compared to simple landscapes

(Mitchell et al. 2014). Furthermore, the same authors demonstrated that wider soybean fields decrease the abundance and richness of aphidophagous predators and herbivores of soybean (Mitchell et al. 2014). Maisonhaute et al. (2017) found that cumulative soybean aphid abundance is explained by the combined effect of natural enemy and landscape variables, rather than by natural enemies alone, under high soybean aphid infestation levels in Québec. Therefore, studying patterns of movement of predators between soybean and adjacent habitats is important to understand soybean aphid suppression.

Lady beetles are likely the most effective biological control agents of soybean aphids (Fox et al. 2004; Costamagna and Landis 2007). Woltz and Landis (2013) demonstrated that manipulating levels of lady beetle immigration to plots with aphids significantly affects the level of soybean aphid suppression observed in soybean fields. Previous work has studied lady beetle movements within and between crops, using mark-release-recapture techniques (e.g. Ives 1981; van der Werf et al. 2000; Hagler and Naranjo 2004) and stable isotope analysis (di Lascio et al. 2016). Using paint mark on the elytra, van der Werf et al. (2000) found that *C. septempunctata* have longer dispersal and short residence times when aphids are not abundant in alfalfa, *Medicago sativa* L. in Utah. Using similar marking techniques, Ives (1981) shows that *C. californica* Mannerheim and *C. trifasciata* Mulsant (Coleoptera: Coccinellidae) move regularly between alfalfa and oats, *Avena sativa* L., and their crop preference depends on the prey density in each crop. Using two protein-marking enzyme-linked immunosorbent assays (ELISA), Rabbit immunoglobulin G (IgG) and chicken IgG, Hagler and Naranjo (2004) observed that *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) moved in greater numbers from cantaloupe, *Cucumis melo* L., to cotton, *Gossypium* sp. L., than vice versa, in Arizona. Using stable isotope analysis, di Lascio et al. (2016) found that patterns of movement of

C. septempunctata, *Propylea quatuordecimpunctata* L., and *Hippodamia variegata* Goeze (Coleoptera: Coccinellidae) between alfalfa and corn fields depend on lady beetle species identity in Spain.

To date, there have been no studies that tracked movement of lady beetles between soybean and other crops or neighbouring habitats in North America. I conducted a mark-release-recapture (MRR) study of *C. septempunctata* between soybean and alfalfa to gather detailed information on the short-term movement of this species across habitat boundaries in agroecosystems. Alfalfa provides a reservoir of many insect natural enemies in agricultural landscapes in Australia (Hossain et al. 2001; Pearce and Zalucki 2005; Pearce and Zalucki 2006) and North America (Elliott et al. 2002; Snyder and Ives 2003). As a perennial crop, alfalfa harbours several aphid species throughout the growing season and natural enemies show numerical responses to aphid densities in alfalfa in eastern South Dakota (e.g. Elliott et al. 2002). In Manitoba, several species of lady beetles, green lacewings, damsel bugs, minute pirate bugs and ground beetles (Coleoptera: Carabidae) are commonly found in alfalfa (Uddin 2005). Costamagna et al. (2015) found that melon aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae), suppression is positively associated with higher proportions of alfalfa in the landscape in Australia, suggesting that alfalfa act as a source of predators in those agricultural landscapes.

The benefits of having predators to regulate aphids in agroecosystems have long been recognized but studies on the movement of aphidophagous predators between soybean and adjacent habitats are limited (e.g. González et al. 2016). The primary goal of this study was to quantify the movement of aphidophagous predators between soybean and adjacent habitats. Specifically, the objectives were 1) to determine the movement directionality (i.e. immigration

and emigration) of predators between soybean and adjacent habitats and 2) to quantify the movement behaviour (i.e. flight direction, displacement distance, and speed) of the common seven-spotted ladybird beetle, *C. septempunctata*, within and between soybean and alfalfa.

Methods

Sampling movement of predators between soybean and adjacent habitats

Patterns of predator movement between soybean and adjacent fields were studied in 12 (2013) and 15 (2014) fields in 12 localities in Manitoba: Altona, Arnes, Carman, Elm Creek, Emerson, Gimli, Glenlea, La Broquerie, Letellier, Morris, Rosewood, and Warren. In each focal soybean field, at least one type of adjacent habitat was sampled representing the most common crop and non-crop borders in Manitoba (Appendix I). A total of 30 field borders were studied including alfalfa (n = 7), canola (*Brassica napus* L.; n = 7), wheat (*Triticum* spp. L.; n = 3), border-grass (Family: Poaceae; n = 2) and woodland (n = 11; Appendix VI). Townes style bi-directional Malaise traps (dimensions: 190 cm height at front, 160 cm length and 110 cm height at back; Sante Traps, Lexington KY, US) were established in each soybean field border to measure immigration and emigration of predators. Fourteen traps were established in 2013 and 16 traps in 2014 (see Appendix VI). In 2014, eight additional traps were deployed in eight soybean fields (100 m from the field border) as controls to compare movement patterns between and within habitats (Appendix VI). The two collection bottles of each bi-directional Malaise trap were filled with 70% ethanol (~375 ml) and were changed weekly from 22nd July to 16th August in 2013 (3 weeks) and from 28th July to 28th August in 2014 (4 weeks). Captures during the two initial weeks of both years were used for analyses presented in Chapter 3. All traps were inspected weekly for damage due to wildlife, wind, and rain; though no damage was observed during this study. All captured insects were stored in containers (0.94 L, Plastipak Industries Inc.,

Boucherville, Québec, Canada) with 70% ethanol for later identification. Aphidophagous predators were identified to family (Coccinellidae, Chrysopidae, Hemerobiidae, Nabidae, Anthocoridae, and Syrphidae) and species when possible, using taxonomic keys (Garland 1985; Vockeroth 1992; Silveira et al. 2003; Acorn 2007; Miranda et al. 2013) and their abundances were recorded for each sample (Appendix VII). For hover flies and few green lacewing species identities were confirmed by taxonomists at the Canadian National Collection of Insects, Arachnids and Nematodes. Voucher specimens of predators were deposited in the Wallis-Roughley Museum of Entomology, University of Manitoba, Canada. Flowering times in adjacent canola fields were recorded during the weekly sampling (Appendix VIII).

Mark-release-recapture study

Two mark-release-recapture (MRR) experiments were carried out in commercial soybean and alfalfa fields in Gimli (50°34'55.0"N, 97°00'36.9"W) from 10 to 12 July in 2013 and in the Ian N. Morrison Research Farm, Carman (49°30'06.3"N, 98°01'34.9"W) from 23 to 25 July in 2014. Field sites were selected to ensure soybean and alfalfa plants had similar heights during the experimental period (see results) and there were no barriers between fields. Soybeans fields had similar row spacing (50 cm) in both years. Alfalfa fields used for this study was for hay cut. Adult seven-spotted lady beetles, *C. septempunctata*, were used for this study as they were the most abundant lady beetle species found in Manitoba (Uddin 2005). Lady beetles were collected two days prior to each experiment by sweep-netting in alfalfa and wheat fields at the Glenlea Research Station of the University of Manitoba. Captured lady beetles were transferred into ventilated containers (11.5 cm diameter × 14 cm height, Bug Tub Inc., Lacombe, AB, Canada) and the containers were transported to the laboratory in coolers at 5 °C (90 cm × 30 cm × 30 cm, The Coleman Company Inc., Wichita, KS, USA). Lady beetles were kept at 5 °C for 24 h, and

then were transferred into Petri dishes on an ice covered plastic basin (40 cm × 30 cm × 10 cm) to immobilize them during marking with paint markers (Extratine, Decocolor Opaque Paint marker, Uchida of America Corporation, Barcodes: 028617141015 for 140-S light blue markers and 028617140513 for 140-S yellow markers). Lady beetles were painted on their elytra with one of six different combinations of colours (light blue or yellow) and patterns of spots to indicate release points (Figure 6). Marking each lady beetle took approximately five seconds and was followed by five minutes at room temperature to allow the paint to dry. After marking, lady beetles were transferred to ventilated containers (≤ 28 lady beetles/container; 4 containers/release point) that were kept in a room at 5 °C for 24 h until release. Preliminary laboratory experiments confirmed that storage temperatures and marking procedure did not affect survivorship of the lady beetles (Appendix IX) and observations suggested it did not affect their flight behaviour (K.G.L.I.S., personal observation). To reduce disturbance-induced dispersal, all marked lady beetles were released at 10.00 a.m. on 12 July 2013 and at 9.00 a.m. on 23 July 2014, when air temperatures were still cool (van der Werf et al. 2000). Periodic inspections of release points were conducted during the initial two hours after release, ensuring that lady beetles were leaving the containers and no predators were attacking them.

Sampling design protocol

Three lady beetle release points in alfalfa (aa, bb, and cc, Figure. 6) and three release points in soybean (gg, hh, and ff) were established 12 m from the soybean-alfalfa border. A previous MRR study found that 30 m was the maximum recapture distance for *C. septempunctata* in alfalfa after 24 hours (van der Werf et al. 2000). Therefore, in my study the release points were established 12 m from the soybean-alfalfa border in order to ensure lady beetles could move between fields within a day. The number of marked lady beetles released at each point was based

on the total number of lady beetles available for the experiment. A total of 654 and 600 marked lady beetles were released in 2013 and 2014, respectively. In each year, an equal number of marked lady beetles were released at each of the six release points.

The sampling area consisted of a rectangular area that spanned both the alfalfa and the soybean fields (Figure 6). Seven transects (A-G) separated by 4 m were laid out perpendicular to the soybean-alfalfa field border. This separation prevented overlap between adjacent sweep-net sampling strips along transects. Sampling points along transects were established at 3 m intervals. Results from the 2013 experiment indicated that the maximum distance at which lady beetles were recaptured between crops exceeded the maximum distance sampled within each crop. To avoid bias in the comparisons, in the 2014 experiment, transect length was increased from 72 m (2013) to 102 m (increasing total recapture points from 168 to 238, respectively). Five sweeps in a full 180-degree arc were taken between two sampling points along transects (Figure 6) and the number of marked and unmarked lady beetles were recorded at each point. Captured lady beetles were released immediately after counting. The original release point for each of the recaptured beetles was determined by their mark. Sweep-net samples along transects were taken 2, 4, 6, 8, 24, 26, 28, 30, 32 and 48 hours after the release. To avoid bias, individuals sampling were randomly assigned a maximum of two transects in each sampling period.

In addition to the sweep-netting, 6 (2013) and 10 (2014) Townes style bi-directional Malaise traps were established at the border between alfalfa and soybean (4 m away from the two outer transect lines A and G, Figure 6). Collection bottles were filled with soapy water (~350 ml) and replaced every 24 hours during the study period. Marked and unmarked lady beetles captured in the traps were identified and recorded separately for each trap. At the same time, sampling of field populations of aphids and aphidophagous predators in each field was

conducted using standard sweep-net sampling (25 sweeps/sample, six samples/field). Each sweep-net sample was placed in a Ziploc polyethylene bag (30 cm × 40 cm), transported to the laboratory using coolers at 5 °C, and stored at -18 °C for the later identification. Aphidophagous predators and aphids captured in sweep-net samples were identified to family level and their numbers were recorded. Plant height, vegetative and reproductive stages were recorded using 30 randomly selected plants each year. Quadrat sampling (1 m² quadrats; 30 quadrats/field) was carried out to measure the percentage of vegetation cover. Plant counts, sweep-net sampling and quadrat sampling were conducted outside the MRR sampling area to avoid disturbance. During the sampling period, temperature, precipitation, wind direction and wind speed were obtained from the nearest weather stations (Gimli Industrial Park Airport Weather Station and University of Manitoba Carman Weather Station; Appendix X).

Data Analysis

Captures of predators moving between soybean and adjacent habitats

Linear mixed-effect models were used to test the effects of adjacent border (alfalfa, canola, border-grass, woodland, and wheat), sampling year (2013 and 2014) and directionality predator movement (i.e. immigration versus emigration to soybean) and their 2- and 3-way interactions on the number of predators captured on each side of the BMT. Since immigration and emigration were quantified in the same trap, direction of movement was nested within trap, which was modeled as a random effect. All aphidophagous predators combined (i.e. total aphidophagous predators) and totals per family (i.e. Coccinellidae, Syrphidae, Nabidae, Anthocoridae, Chrysopidae, and Hemerobiidae), were used as response variables in separate models. Counts were averaged per bottle and per day to account for different number of weeks sampled each year and different sampling intervals that occurred in some weeks due to rain events. Counts

were log-transformed ($\log_{10} [\text{counts} + 1]$) before analysis, to meet model assumptions. Stepwise backward selection was used to select the best final model by deleting non-significant interaction terms to improve model fit. Linear mixed-effect models were fit using the function “lme” in the library “nlme” (Pinheiro et al. 2016) in R (R Development Core Team 2016). The significance of interaction terms was tested using the ‘anova’ function on maximum likelihood estimates of model parameters to obtain p -values from likelihood ratio tests (Pinheiro and Bates 2006), and the level of improvement of the model was estimated using Akaike Information Criterion (AIC). Contrasts of least-squares means adjusted by the Tukey method for multiple comparisons were used to conduct pairwise comparisons between treatments within significant 2-way interaction terms, using “lsmeans” function in the “lsmeans” package (Lenth 2016) in R (R Development Core Team 2016). Either paired t-tests or paired Wilcoxon rank sum tests with continuity corrections were used to compare numbers moving towards the field interior with numbers moving towards the field margin in control BMT, and combined movement (i.e. average immigration and emigration) between control and border BMT.

Mark-release-recapture study

The displacement distance by recaptured beetles was calculated as a straight line between the release and the recapture points. Travel speed was calculated as displacement distance/time between release and recapture points. Due to the changes in the sampling design that resulted in variable maximum travel displacement distances monitored within and between fields, separate analyses were conducted per year.

The number of recaptured lady beetles in sweep-net samples was compared within and between crops with Kruskal-Wallis rank sum tests with pairwise comparisons adjusted by the Sequential Bonferroni method (Rice 1989). All samples that yielded zero lady beetles in

equivalent positions in the soybean and the alfalfa fields were eliminated to simplify statistical analysis. Similarly, to match positions with captures in the opposite field and have the same number of observations in each field, five samples with zero lady beetles were maintained. Either paired t-tests or one sample t-tests (when there was a zero capture in one treatment) were used to compare the directionality of lady beetles captured in bi-directional Malaise trap samples. Due to the different maximum distance at which lady beetles were sampled within and between crops, separate analyses were conducted for displacement distances and speed results, using either two sample t-tests, Wilcoxon rank sum test with continuity correction or one sample t-tests. One-way ANOVA was used to compare predator abundance in sweep-net samples, plant height, and percentage of vegetation cover between alfalfa and soybean within and between years. For all parametric tests, normality of the data and homogeneity of variance were visually checked using normal Q-Q plots and heteroscedasticity plots (i.e. fitted values vs. residuals). All analyses were completed using R (R Development Core Team 2016). Unless otherwise indicated, all reported values are mean \pm SEM, and $\alpha = 0.05$ was used to assess significant differences.

Results

Predators moving between soybean and adjacent habitats

A total of 25,460 aphidophagous predators (including adult stages of species that are predatory as juveniles) were captured moving between soybean and adjacent habitats using bi-directional Malaise traps; with an average of 13.18 ± 1.25 individuals/bottle/day. The aphidophagous guild included six insect families and was dominated by Syrphidae (hover flies, 89.75% of total capture, 12.21 ± 1.22 number of individuals/bottle/day), followed by Anthocoridae (4.56%, 0.62 ± 0.07), Coccinellidae (1.27%, 0.18 ± 0.02), Chrysopidae (green lacewings, 0.64%, 0.09 ± 0.01), Hemerobiidae (brown lacewings, 0.58%, 0.08 ± 0.01), and Nabidae (damselflies, 0.04%, 0.005

± 0.002) (Appendix VII). *Toxomerus marginatus* (Say) (Diptera: Syrphidae) represented 94.55% of the aphidophagous hover flies, *C. septempunctata* represented 60.07% of the lady beetles and *Chrysoperla carnea* (Stephens) represented 72.20% of the green lacewings.

Overall captures of predators were higher in 2014 (16.76 ± 1.68 individuals/bottle/day, $n = 192$) than in 2013 (4.98 ± 1.08 , $n = 84$; Table 3). There was no difference between emigration (14.72 ± 2.58 individuals/trap/day, $n = 106$) and immigration (12.78 ± 1.73) of total predators between soybean and adjacent habitats or among field borders (Table 3). However, movement direction varied among field borders (Table 3). Captures from soybean to canola were higher than to woodlands and movement levels to all other borders were intermediate (Figure 7a). There was no difference in immigration levels to soybean among field borders (Figure 7a). Emigration to canola and immigration from woodland were significantly higher than movements in the opposite direction (Figure 7a). The directionality of total predator movement did not differ in other field borders sampled. Aphidophagous hover flies were the numerically dominant predator group and consequently they show the same pattern as all predators combined, with higher captures in 2014 (18.41 ± 2.29 individuals/bottle/day, $n = 128$) than in 2013 (4.73 ± 1.07 , $n = 84$; Table 3); higher captures from soybean to canola than from soybean to woodland habitats; higher emigration to canola; and higher immigration from woodland (Figure 7b). Aphidophagous green lacewing captures were similar in both years, but the directionality of movement differed among field borders only due to higher emigration to adjacent canola (Table 3; Figure 7c). Overall, immigration of lady beetles to soybean (0.19 ± 0.04 individuals/trap/day, $n = 106$) was higher than emigration (0.12 ± 0.03 , $n = 106$) and was higher in 2014 (0.20 ± 0.04 individuals/bottle/day, $n = 128$) than in 2013 (0.07 ± 0.01 , $n = 84$), but varied among adjacent habitats to soybean (Table 3). Captures of lady beetles were higher in alfalfa and wheat borders

in 2014 than in 2013 (Figure 8). In 2014, captures of lady beetles were higher in alfalfa and wheat borders compared to canola and woodland, and intermediate in grass borders (Figure 8). There were no differences in captures of lady beetles among habitats adjacent to soybean in 2013 (Figure 8). Captures of minute pirate bugs were higher in 2014 (0.72 ± 0.11 individuals/bottle/day, $n = 128$) than in 2013 (0.03 ± 0.01 , $n = 84$; $F_{1,20} = 27.95$, $p < 0.001$), but did not differ among borders ($F_{4,20} = 2.47$, $p = 0.08$), or between movement directions ($F_{1,29} = 0.13$, $p = 0.71$; Appendix XII). Similarly, captures of brown lacewings were higher in 2014 (0.11 ± 0.02 individuals/bottle/day, $n = 128$) than in 2013 (0.03 ± 0.01 , $n = 84$; $F_{1,24} = 7.97$, $p = 0.009$), but did not differ among borders ($F_{4,24} = 1.43$, $p = 0.25$), or between movement directions ($F_{1,29} = 2.14$, $p = 0.15$). Captures of damsel bugs did not differ among borders ($F_{2,22} = 0.14$, $p = 0.87$), between movement directions ($F_{1,22} = 1.22$, $p = 0.28$), or years ($F_{1,22} = 2.58$, $p = 0.12$).

In control traps located 100 m from the field border, there was no significant difference between the two sides of the trap for the capture of all predators combined (Figure 7a), and each predator group separately (separate paired t-tests per group, all $p > 0.05$), except for brown lacewings ($t = 3.32$, $df = 31$, $p = 0.0023$) (Appendix XII). Combining movement direction per trap (i.e. average of emigration and immigration) revealed similar quantities of all predators combined in control traps (11.3 ± 2.3 individuals/bottle/day) and in border traps (13.3 ± 3.0 ; $t = 0.88$, $df = 31$, $p = 0.39$). Separate predator groups also showed no differences in overall movement between border and control (data not shown).

Mark-release-recapture study

In the MRR experiment, 38 seven spotted beetles (5.8 % of released individuals) and 34 (5.7 %) were recaptured in 2013 and 2014, respectively. Movement of lady beetles differed within and

between crops in 2013 (Kruskal-Wallis $\chi^2 = 17.20$, $df = 3$, $p < 0.001$) and 2014 (Kruskal-Wallis $\chi^2 = 9.70$, $df = 3$, $p < 0.05$). In 2013, approximately one quarter of recaptured individuals moved from soybean to alfalfa than within crop, and no individuals released in alfalfa were captured in soybean (Figure 9a; Appendix XI). In 2014, captures of marked lady beetles from soybean to alfalfa were at the same level of captures within crops, but were higher than captures of lady beetles moving from alfalfa to soybean (Figure 9b; Appendix XI). Bi-directional Malaise trap samples showed a similar pattern of higher captures of lady beetles moving from soybean to alfalfa, although it was significant only in the second year of study (2013: paired $t = 1.40$, $df = 5$, $p = 0.22$; 2014: one sample $t = 3.28$, $df = 19$, $p < 0.05$; Figure 10).

The greatest displacement distances recorded from recaptured marked lady beetles were 33 m after 4 h and 52.4 m after 28 h in 2013 and 2014 respectively, both from soybean to alfalfa. The maximum displacement distances recorded within alfalfa were 12 m after 4 h and 24.3 m after 32 h, and within soybean 8.5 m and 18.4 m in 2013 and 2014 respectively. In 2013, mean displacement of ladybeetles was higher within alfalfa than within soybean (two sample $t = 2.54$, $df = 31$, $p = 0.02$; Figure 9c). The same trend was observed for displacement distances in 2014, but it was not significant (two sample $t = 1.77$, $df = 10$, $p = 0.11$; Figure 9d). Longer displacement distances were observed from soybean to alfalfa than vice versa in both years (2013: one sample $t = 9.08$, $df = 2$, $p = 0.01$; 2014: two sample $t = -3.71$, $df = 11$, $p = 0.0003$; Figures 9c and 9d).

The highest speeds recorded from recaptured marked lady beetles were 8.25 mh^{-1} (2013) and 18.34 mh^{-1} (2014), both for beetles that moved from soybean to alfalfa. In 2014, lady beetles moved faster from soybean to alfalfa than vice versa ($W = 0$, $p = 0.03$; Figure 9f). The same trend was observed for speeds recorded in 2013, but it was not significant (one sample $t = 3.63$,

df = 2, $p = 0.07$; Figure 9e). Higher speeds were recorded within alfalfa than in soybean in 2013 (two sample $t = 2.20$, df = 31, $p = 0.04$; Figure 19e). The same pattern was observed for speeds within crops in 2014, but it was not significant ($W = 45$, $p = 0.35$; Figure 9f).

Two aphid species were recorded in alfalfa fields: pea aphids, *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae, 97.7% of total aphids) and spotted alfalfa aphids, *Therioaphis maculata* (Buckton) (Hemiptera: Aphididae, 2.3%). Combined aphid populations were higher in 2014 (210.33 ± 61.65 aphids/25 sweeps) than in 2013 (58.33 ± 9.41 aphids/25 sweeps; two sample $t = -2.43$, df = 10, $p < 0.05$). No aphids were observed in the soybean fields studied. Low numbers of aphidophagous predators were found using sweep-net sampling and, predator abundance was slightly higher in alfalfa than in soybean (2013: alfalfa 2.33 ± 0.71 individuals/25 sweeps, soybean 0.33 ± 0.33 , $F_{1,10} = 6.43$, $p = 0.03$; 2014: alfalfa 3.50 ± 1.09 , soybean 0.33 ± 0.21 individuals/25 sweeps, $F_{1,10} = 8.17$, $p = 0.02$).

Plant heights of both soybean and alfalfa were greater in 2014 than 2013 (soybean: 25.50 ± 0.24 cm in 2013, 43.64 ± 0.89 cm in 2014, $F_{1,58} = 386.1$, $p < 0.001$; alfalfa: 24.97 ± 0.13 cm in 2013, 41.30 ± 1.36 cm in 2014, $F_{1,58} = 142.4$, $p < 0.001$). However, similar plant heights were recorded between crops within the same year (2013: $F_{1,58} = 3.67$, $p = 0.06$; 2014: $F_{1,58} = 2.06$, $p = 0.16$). The percentage vegetation cover in soybean was higher than alfalfa in both years (2013: soybean 61.83 ± 2.76 %, alfalfa 42.33 ± 2.27 %, $F_{1,58} = 29.77$, $p < 0.001$; 2014: soybean 65.50 ± 2.88 %, alfalfa 39.10 ± 3.03 %, $F_{1,58} = 39.83$, $p < 0.001$), but similar vegetation covers were recorded in the same crop type between years (soybean: $F_{1,58} = 0.85$, $p = 0.40$; alfalfa: $F_{1,58} = 0.78$, $p = 0.36$).

Discussion

My results indicate that the directionality of predator movement in soybean borders is significantly affected by the identity of adjacent habitats, supporting previous findings in other agroecosystems (Duelli et al. 1990; Macfadyen and Muller 2013; Macfadyen et al. 2015). The overall pattern of movement of all aphidophagous predators combined was the same as that for hover flies, the dominant predator group in the assemblage. The levels of hover fly emigration from soybean differed among the adjacent habitats as they emigrated to canola in greater numbers compared to adjacent woodlands, and at intermediate levels to other habitats. Low number of aphids in the soybean fields studied (Chapter 3 results), and diminishing nectar resources in soybean fields that were reaching the end of the flowering period (Appendix I), could explain the pattern of hover fly movement observed. Having flowering canola fields adjacent to soybean could explain why soybean was a source of hover flies to canola until the 3rd week of the experiment (Appendix VIII), where they also facilitate pollination (Schneider 1969; Bugg et al. 2008; Jauker and Wolters 2008). Hover flies search for flowering plants to obtain nectar and pollen to fulfill their nutritional requirements (e.g. Kevan and Baker 1983; Tooker et al. 2006). Hover flies immigrated in greater numbers from adjacent woodland habitats to soybean. Similarly, a study conducted in Australia showed that higher number of hover flies moved from native vegetation to adjacent barley and wheat in greater numbers (Macfadyen et al. 2015), suggesting that woodlands may be a good source of hover flies in the agricultural landscape.

The hover fly, *T. marginatus*, was the numerically dominant aphidophagous species that moved between soybean and the surrounding habitats. Previous studies showed that *T. marginatus* is the numerically dominant hover fly species in soybean fields, including studies

performed using sticky cards and sweep-net samples in east-central Minnesota (Eckberg et al. 2015), and using pan traps, sticky cards and sweep-net samples in central Iowa (Gill and O'Neal 2015). In contrast, Kaiser et al. (2007) and Noma and Brewer (2008) found that *Allograpta obliqua* Say (Diptera: Syrphidae) is the most abundant hover fly species found in soybean fields in Michigan, but this species was not abundant in my study area. Kaiser et al. (2007) found that larvae of *T. marginatus* feed on two aphid species, *A. glycines* and *Acyrtosiphon* sp. (Hemiptera: Aphididae) on Fabaceae plants. Laboratory studies indicate that a larva of *T. marginatus* can kill 132 lettuce aphids, *Nasonovia ribisnigri* Mosley (Hemiptera: Aphididae) during its larval stage of approximately 15 days (Hopper et al. 2011), suggesting that this species can cause high mortality on aphid colonies. Wheelock et al. (2016) found that *T. marginatus* was the dominant pollinator in soybean and corn fields in Iowa. Altogether, these results suggest that hover flies may provide multiple benefits to soybean and canola, including pest control and pollination services (Ssymank et al. 2008).

Green lacewings and hover flies require similar resources, and they showed similar patterns of movement in soybean borders. Adult green lacewings are likely to feed on pollen and nectar from flowering canola (McEwen et al. 2007). Duelli (1980) demonstrated that aphid honeydew volatiles increase landing of *C. carnea* on alfalfa and influence their movement toward the source of these kairomones after landing. Gavloski et al. (2011) reports several aphid species including, the cabbage aphid (*Brevicoryne brassicae* (Linnaeus)), the green peach aphid *Myzus persicae* (Sulzer), and the turnip aphid (*Lipaphis erysimi* (Kaltenbach)) (Hemiptera: Aphididae) associated with different phenological stages of canola throughout the growing season in Canada, and several predator groups associated with them, including various species of green lacewings, lady beetles and hover flies (Gavloski et al. 2011). Furthermore, El Arnaouty et

al. (1996) demonstrated that *C. carnea* can kill 140 second-instar nymphs of green peach aphid, *M. persicae*, during its larval life, and larva of *Chrysoperla nipponensis* (Neuroptera: Chrysopidae) can consume 43.3 mg (wet weight) of *M. persicae*, suggesting that green lacewings are voracious predators of aphids. Therefore, green lacewings have the potential to provide pest control services also to canola. The movement of hoverflies and green lacewings should also be studied at non-flowering periods of canola and soybean, to determine their season-long movement patterns.

In the year of highest lady beetle abundance recorded (2014), movement was higher in adjacent alfalfa and wheat habitats compared to canola and woodland habitats. Macfadyen and Muller (2013) found that coleopteran and neuropteran predators moved more frequently from cereal fields (wheat/barley) to canola fields late in the season, suggesting that predators are frequently associated with cereals early in the season. Several aphid species are found in wheat fields in Manitoba, including the English grain aphid *Sitobion (Macrosiphum) avenae* Fabricius, the bird cherry-oat aphid *Rhopalosiphum padi* (Linnaeus), and the greenbug *Schizaphis graminum* (Rondani) (Hemiptera: Aphididae; Bakker 1974; Gavloski and Meers 2011; Gavloski 2015a). In addition, previous studies have shown that several aphids are commonly reported in wheat fields from July to August in Manitoba (Malyk and Robinson 1971; Bakker 1974), and lady beetles are frequently associated with wheat fields (Bakker 1974; Gavloski and Meers 2011). Several aphids also occur in alfalfa, which is known as a reservoir for many predators, including lady beetles (e.g. Elliott and Michels 1997; Stephens and Losey 2004). Schmidt et al. (2007b) found that soybean grown with an alfalfa living mulch enhances predator diversity and abundance, and increases the suppression of soybean aphids compared to a soybean monoculture. Movement levels of lady beetles are influenced by the availability of aphids in

wheat and alfalfa at different phenological stages (Hodgson 2007; Gavloski and Meers 2011; Hodek et al. 2012). These results suggest that alfalfa and wheat fields in proximity to soybean fields may contribute to increased soybean aphid suppression.

The results of the MRR experiments also suggest that alfalfa is a good habitat for lady beetles, with individuals dispersing greater numbers from soybean to alfalfa. A potential explanation for the net movement to alfalfa could be the abundance of pea aphids and spotted-alfalfa aphids, and the absence of aphids in soybean. Wind direction was not a factor for the major movement flow of marked lady beetles from soybean to alfalfa as wind blew from alfalfa to soybean in both years (Appendix X). Ives (1981) used MRR methods to study the abundance and movement of lady beetles between alfalfa and oat plots in British Columbia, Canada. He showed that the two lady beetle species studied move between crops, but *C. trifasciata* prefers alfalfa and *C. californica* prefers oat. Movement of both species was affected by aphid density in the plots and by temperature. van der Werf et al. (2000) found in another MRR study that *C. septempunctata*, moved greater distances and stayed shorter times when aphids were not abundant in alfalfa, even in sugar sprayed plots. Lady beetles use “resource mapping” and leave crops to evaluate the quality of the surrounding habitats (Hodek et al. 2012). Cardinale et al. (2006) found that after arriving to a habitat, lady beetles decide to stay or leave based on the availability of prey and signals from conspecific larvae. This could explain the small number of marked lady beetles that moved from alfalfa to soybean in my study. Movement monitored with BMT in the landscape study showed no directionality of predator movement between alfalfa and soybean borders, suggesting that predators constantly moved between these two crops, supporting previous findings in alfalfa (van der Werf et al. 2000). Altogether, these findings suggest that alfalfa may supply predators to adjacent soybean fields with aphid infestations and

could be an important habitat to maintain in landscapes to maximize pest control services to soybean.

Directionality in control traps (located 100 m from the border) of soybean fields was not significantly different for all predators combined or for most predator groups separately, suggesting that the difference in directionality observed in border BMT was due to the influence of adjacent habitats. Only brown lacewings showed differences in directionality in control traps, and these were on the same direction as the differences in movement direction observed in the border of the same fields, suggesting that the pattern of movement may have been influenced by wind direction (data not shown). More studies with higher capture rates of brown lacewings are needed before a clear pattern of movement in relation to different adjacent habitats can be elucidated for these predators. These results also suggest that the quantities of predators crossing the field borders represent the quantities of predators foraging in the interior of soybean fields (at least within a 100 m from the field border).

Studies that quantified agricultural landscape complexity have suggested that woodlands are an important sources of predators to crops (Duelli and Obrist 2003; Bianchi et al. 2006). Previous studies showed that decreasing proximity to woodlands and increasing amount of wooded areas in the landscape increase predator richness and abundance in crops, including soybean (Chaplin-Kramer et al. 2011; González et al. 2015). Lady beetle abundance also increases in soybean fields located in complex landscapes associated with more forests and grasslands areas (Gardiner et al. 2009a; Woltz and Landis 2013). Few studies measured the movement of predators directly in relation to woodlands. Hover flies, green lacewings, minute pirate bugs, lady beetles, and brown lacewings showed patterns of higher movement from woodland to soybean, than vice versa, although it was significant for the first predator group

only, probably due to the low captures by BMT observed in the other groups. A study using BMT in Córdoba province, Argentina suggested that coleopteran predators move from forest to soybean in greater numbers than vice versa, and movement of predators decreases with senescence of soybean (González et al. 2016). Macfadyen et al. (2015) found that lady beetles, adult hover flies and brown lacewings moved in greater numbers and more often from native vegetation to adjacent crop fields (i.e. barley and wheat) in New South Wales and Queensland, Australia. In contrast, Macfadyen and Muller (2013) found no differences between immigration and emigration of hover flies and lady beetles between native perennial vegetation and canola in New South Wales, Australia. In summary, my results provide empirical evidence that woodlands function as a source of predators to crops, supporting previous results of landscape scale studies and quantifications of predator movement in other systems. However, the numbers of predators captured were low and their importance to pest suppression seems lower than for predators from other habitats (see chapter 3). More studies at different times of the season are needed to fully understand the role of woodlands as potential sources of aphidophagous predators to crops.

My study contributes empirical evidence to the growing body of literature that suggests that movement of predators to crops vary with predator identity and with the type of adjacent habitat (Duelli et al. 1990; Macfadyen and Muller 2013; Macfadyen et al. 2015; González et al. 2016), which in turn affects pest suppression (Schellhorn et al. 2014; Costamagna et al. 2015). Farmers, policy makers and stakeholders could incorporate this knowledge to choose which crops should grow near suitable habitats to enhance natural biological control of pest via increasing the movement of suitable natural enemies into particular crops. Future studies should investigate how crop phenology influences the seasonal pattern of movement of predators, particularly due to the fluctuation of prey and other resources at various times of the season, in

order to maximize the temporal availability of resources (e.g. Schellhorn et al. 2014; González et al. 2016). In my study non-crop (e.g. woodlands) and perennial crops (alfalfa) show moderate quantities of predators moving to soybean, suggesting a limited contribution to pest suppression during the time of my experiments. However, these habitats can be important to maintain predator populations early in the season (Bianchi et al. 2006), and studies on the temporal dynamics of predators in these habitats are needed to fully understand their role.

Table 3. Results of linear mixed-effects models for total predators, hover flies, green lacewings, and lady beetles captured in bi-directional Malaise traps, with border (alfalfa, canola, border-grass, woodland, and wheat), migration (immigration to vs emigration from soybean), year (2013 and 2014) and their interactions.

Factor	Total predators				Hover flies				Green lacewings				Lady beetles			
	<i>df</i> _{num}	<i>df</i> _{den}	<i>F</i>	<i>p</i>	<i>df</i> _{num}	<i>df</i> _{den}	<i>F</i>	<i>p</i>	<i>df</i> _{num}	<i>df</i> _{den}	<i>F</i>	<i>p</i>	<i>df</i> _{num}	<i>df</i> _{den}	<i>F</i>	<i>p</i>
Border	4	24	1.52	0.220	4	24	1.49	0.235	4	24	1.35	0.280	4	20	7.76	0.001
Year	1	24	12.48	0.002	1	24	10.37	0.004	1	24	1.36	0.254	1	20	11.19	0.003
Migration	1	25	0.22	0.640	1	25	0.05	0.829	1	25	0.01	0.943	1	29	6.82	0.014
Border × Migration	4	25	6.95	0.001	4	25	5.67	0.002	4	25	2.88	0.043	-	-	-	-
Border × Year	-	-	-	-	-	-	-	-	-	-	-	-	4	20	6.59	0.002

Interactions between Year × Migration and Border × Year × Migration were not significant for any of the four predator variables presented here.

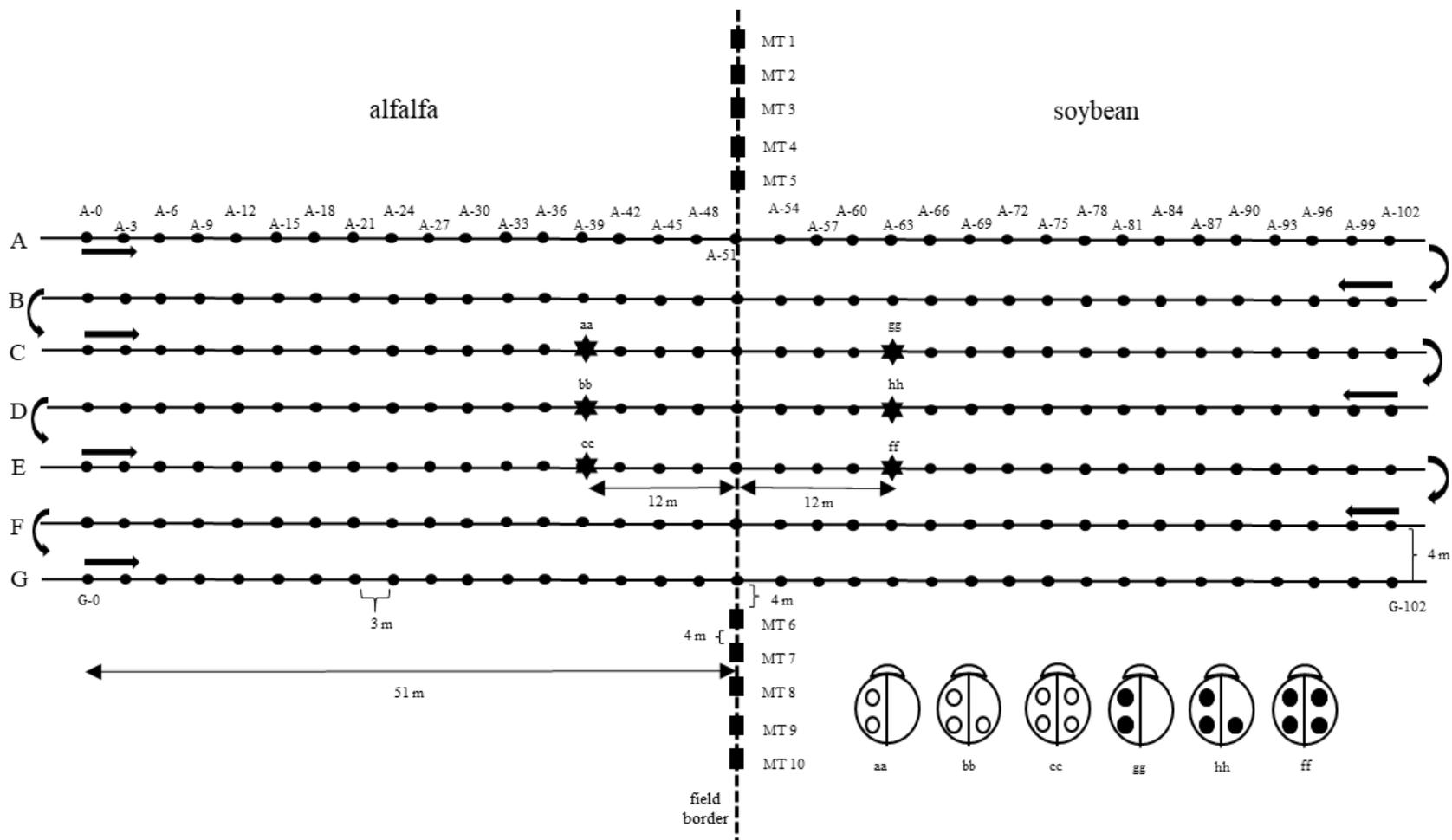


Figure 6. Sampling design for measuring dispersal of lady beetles within and between alfalfa and soybean fields. Seven transects (A-G) were laid out perpendicularly to the alfalfa-soybean field border, with a distance between transects of 4 m. The length of the transects was increased from 72 m in 2013 to 102 m in 2014. Recapture points along transects (e.g. A-0 to A-102) were established

every 3 m and arrows show the sweep-net sampling directions. Stars indicate lady beetle release points in alfalfa (aa, bb, and cc) and soybean (gg, hh, and ff). Lady beetles were marked with unique colour patterns to identify their release points in alfalfa (aa, bb, and cc; light blue) and in soybean (gg, hh, and ff; yellow). Ten bi-directional Malaise traps (MT 1 to MT 10) were established along the soybean-alfalfa field border. Transects were laid perpendicularly to soybean rows in both years.

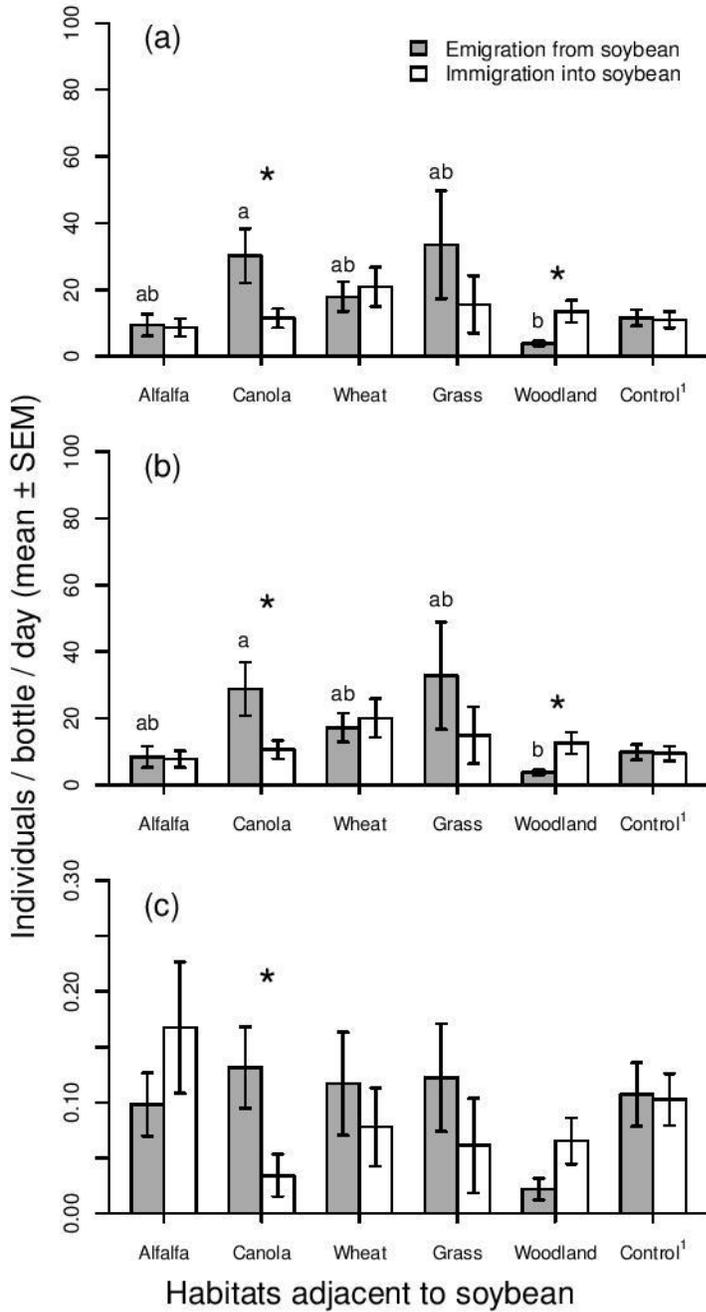


Figure 7. Average daily emigration and immigration of (a) total aphidophagous predators, (b) aphidophagous hover flies, and (c) aphidophagous green lacewings between soybean and different adjacent habitats, combining two years of sampling (7 weeks in total). Sampling consisted of bi-directional Malaise traps established on five adjacent habitats: soybean-alfalfa (n= 24 bottles), soybean-canola (n= 25), soybean-grass (n=7), soybean-woodland (n=39),

soybean-wheat (n=11) and control (soybean fields, 100 m from the field border, n=32; see Appendix VI). Significant differences ($p < 0.05$) between emigration and immigration (or captures towards the field interior and field margin in controls) are indicated with *, and for emigration levels among field borders with different lower case letters; no significant differences were observed in immigration levels. ¹ Control bi-directional Malaise traps were established in a subset of fields in 2014 (n=8 fields).

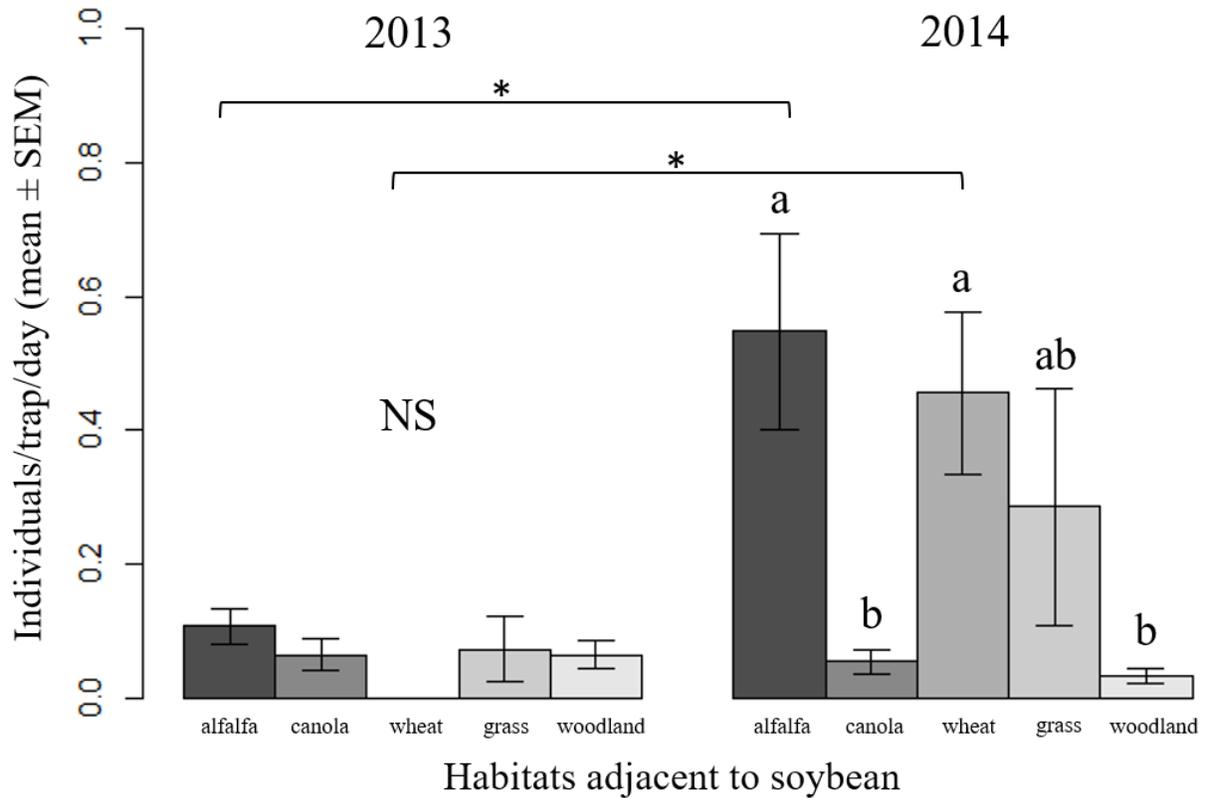


Figure 8. Average daily captures of lady beetles between soybean and different adjacent habitats combining totals from both sides of bi-directional Malaise traps, during 2013 and 2014. Different lower case letters indicate significant difference in captures of lady beetles among adjacent habitats (multiple comparisons of least-square means adjusted by Tukey, $p < 0.05$; NS = not significant) significant differences between years within habitats are indicated by * ($p < 0.05$).

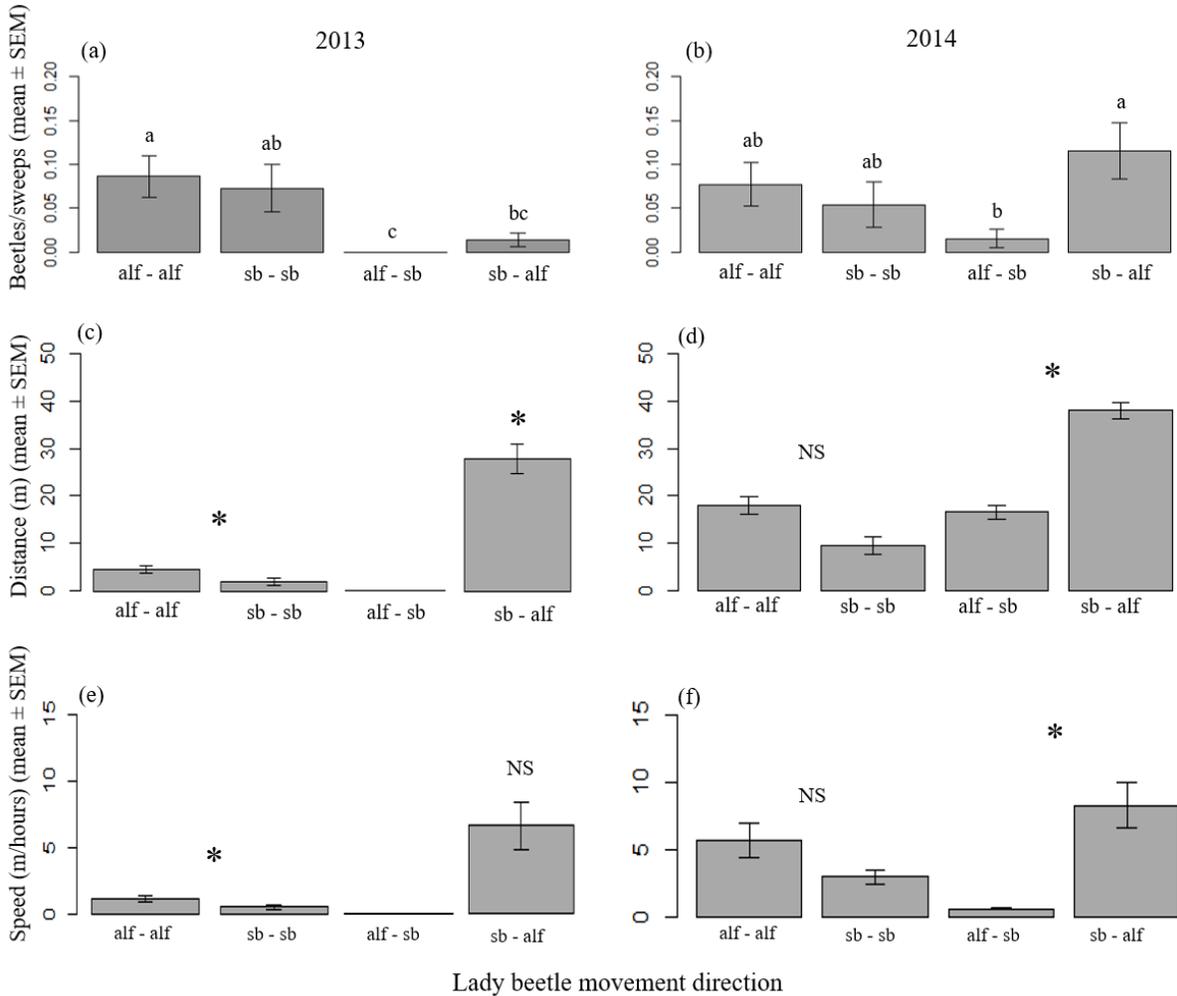


Figure 9. Average captures (a and b), displacement distances (c and d) and speeds (e and f) of marked lady beetles, *C. septempunctata*, within and between soybean and alfalfa fields in 2013 and 2014. Lower case letters represent significant differences ($p < 0.05$) between captures of marked lady beetles within and between fields (overall Kruskal -Wallis test followed by Kruskal -Wallis pairwise comparisons adjusted by Sequential Bonferroni) (a and b). Significance of differences between displacement distances (c and d) and speed of marked beetles (e and f) within and between fields in each year was determined by a two-sample t-test or Wilcoxon rank sum test with continuity correction. When one of the treatments was zero, a one sample t-test with H_0 Mean = 0 was used. * indicates $p < 0.05$; NS = not significant. Movement directions: alf-

alf: alfalfa to alfalfa, sb-sb: soybean to soybean, alf-sb: alfalfa to soybean, sb-alf: soybean to alfalfa.

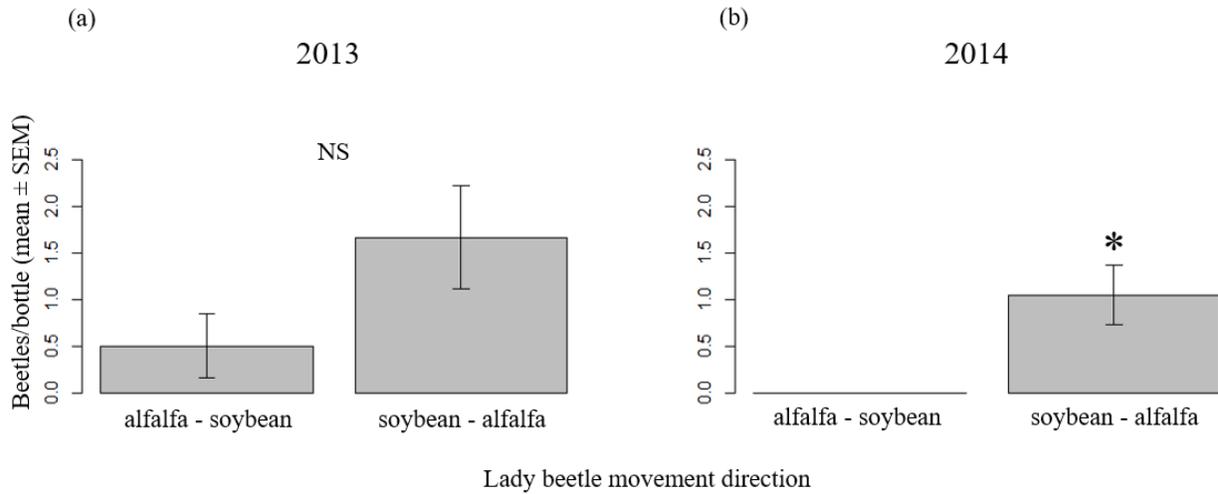


Figure 10. Average total captures of *C. septempunctata*, (i.e. both marked and unmarked beetles) moving between soybean and alfalfa fields in 2013 (a) and 2014 (b). Sampling consisted of 6 (2013) or 10 (2014) bi-directional Malaise traps established on the borders between soybean and alfalfa fields in each year. When one of the treatments was zero, a one sample t-test with $H_0 = 0$ was used. * indicates $p < 0.05$; NS = not significant.

CHAPTER 5: GENERAL DISCUSSION

In agricultural landscapes, land-cover types and predators play an important role in pest suppression (Bianchi et al. 2006). Diverse landscape characters affect the abundance, and diversity of pest and predator populations in crops (reviewed in Chapter 2). The primary goal of this thesis is to gain a better understanding of the contribution of surrounding landscape and predators in the biological control of soybean aphids. The first objective of my thesis was to investigate how soybean aphid suppression is associated with landscape complexity and movement of predators between soybean and adjacent habitats (Chapter 3). For my second objective, I quantified the directionality of predator movements between soybeans and adjacent habitats (Chapter 4).

There is a relatively large and growing body of literature on the association between landscape complexity and pest suppression in agroecosystems, including soybean aphids (reviewed in Chapter 2), but few studies have studied the contribution of predator movements to pest suppression in agricultural landscapes (e.g. González et al. 2016). In Chapter 3, I conducted predator exclusion studies to estimate levels of aphid suppression on soybean aphid sentinel colonies in 27 soybean fields over a two-year period, in Manitoba. I quantified landscape structure by measuring the proportion and diversity of habitats present within 2 km of focal soybean fields and quantified predator movement in soybean field borders using bi-directional malaise traps. In my study, naturally occurring predators suppressed soybean aphids below the economic threshold level of 250 aphids/plant (Ragsdale et al. 2007) in all fields studied. Final aphid population size was reduced by 73.7 % on average in exposed sentinel aphid populations compared to aphid populations protected from predation, a suppression level well within the range observed in previous studies across North America (Koch and Costamagna 2017). Landscape analyses showed that soybean, cereal (wheat, oats, and barley), and canola were the

major land-cover types in the landscapes studied in Manitoba, differing from previously studied landscapes in North America that are typically dominated by corn and soybean (Gardiner et al. 2009a; Noma et al. 2010; Mitchell et al. 2014). The spatial scale of 2 km provided the best supported landscape model, similar to previous studies that found scales between 0.75 and 2 km have the most explanatory power for pest suppression in various agroecosystems (Thies and Tschardtke 1999; Thies et al. 2003; Gardiner et al. 2009a; Noma et al. 2010; Woltz et al. 2012; Rusch et al. 2016). However, when landscape variables were combined with predator movement variables, the best supported model was found at the 0.5 km spatial scale. Surprisingly, the proportions of canola, woodland and field-border grass showed positive associations with final aphid populations in the open treatment. Bi-directional malaise trap and sweep-net sampling indicated that the numerically dominant predators were hover flies (Diptera: Syrphidae), followed by minute pirate bugs (Hemiptera: Anthocoridae) and green lacewings (Neuroptera: Chrysopidae). Immature stages of minute pirate bugs were the dominant species found in sweep-nets and visual soybean plant counts, followed by hover flies, damsel bugs (Hemiptera: Nabidae), and green lacewings.

Studying predator movement between habitats is a growing research area in behavioral entomology, with important consequences for pest suppression in agroecosystems (Chapter 2), but only a few studies have quantified predator movements between crops and adjacent habitats (e.g. Macfadyen and Muller 2013; Macfadyen et al. 2015; González et al. 2016). In my study, overall immigration and emigration from soybean fields did not differ, and therefore predator average movement in the field border was used as predictor of final aphid population size in the open treatment. Green lacewings and lady beetles had negative associations with final aphid population size in the open treatment, whereas brown lacewings showed a positive association

with aphids. Interestingly, the best predictor of aphid abundance was the level of predator movement between soybean and adjacent habitats, either alone or combined with independent landscape composition variables.

Adjacent habitat type did affect the abundance and directionality of predators captured by bi-directional Malaise traps. This is the first study, to my knowledge, to determine the directionality of predator movements between soybeans and adjacent crops (alfalfa, canola, and wheat) and non-crops (woodland and border-grass) using bi-directional Malaise traps. Interestingly, my study shows similar numbers of predators moving through field borders and in interior of the field (i.e. 100 m from the field border), suggesting that predators arriving from adjacent habitats may forage great distances into soybean.

Chapter 4 in this thesis shows that immigration and emigration of predators vary between soybean and adjacent borders. I found that hover flies and green lacewings were captured in higher numbers moving from soybean to canola than vice versa. Hover flies moved in greater numbers from woodland to soybean than vice versa, and green and brown lacewings, lady beetles, and minute pirate bugs showed the same trends. In the year of high predator numbers, I found higher numbers of lady beetles at the alfalfa and wheat borders compared to canola and woodland borders, and intermediate captures at the border-grass border. The mark-release-recapture study indicates that *C. septempunctata* disperse for longer distances from soybean to alfalfa than vice versa, probably due to the absence of *A. glycines* in soybean fields. These results indicate that alfalfa can be a preferred habitat for ladybeetles when aphids are absent in neighboring crops. My findings support previous studies that suggest that lady beetles are very mobile and can quickly move between neighboring crops to aggregate in fields with prey resources (Ives 1981; Ives et al. 1993; van der Werf et al. 2000; Costamagna and Landis 2007).

My findings suggest that adjacent wheat, alfalfa, border-grass, and woodland habitats can be sources of predators to soybeans, and by contrast canola, at least at the time of this study, can function more as a ‘sink’ for predators.

Complex landscapes are usually characterized by a high proportion of natural vegetation, and typically are associated with increased pest suppression (Thies and Tschamntke 1999; Gardiner et al. 2009a; Rand et al. 2012; Rusch et al. 2013). In contrast, my findings (Chapter 3) indicate that an increase in the proportion of woodland in the landscape is associated with higher final soybean aphid population size. In addition, I found relatively low numbers of predators in bi-directional Malaise traps on borders with woodland compared to other borders (Chapter 4). One potential explanation for this could be reduced availability of nectar and nutritious pollen sources in woodlands compared to open grassland habitats, which may result in lower abundance of nectar feeding predators. However, woodlands may still support a small number of predators with the availability of few resources. For example, Alhmedi et al. (2009) found that during the summer stinging nettle plants, *Urtica dioica* L. (Rosales: Urticaceae), present in the ground story of woodlands provide alternative resources for predators, such as aphids, nectar and pollen. In Manitoba, stinging nettle is commonly found in wooded areas (Manitoba Agriculture 2017c), and was observed in adjacent woodland areas in this study (K.G.L.I.S. personal observation).

This thesis suggests that wheat may be a major source of predators associated with soybean aphid suppression, including green lacewings (Chapter 3) and lady beetles (Chapter 4). There was no significant directionality of predator movement at wheat borders, suggesting that wheat does not act as a barrier for predators studied, except for brown lacewings, which were not captured at wheat borders (Chapter 4). These findings are confirmed by the regression models in Chapter 3, increase in the proportion of cereals (wheat, oats, and barley) in the landscape and

captures of lady beetles and green lacewings result in a decrease in soybean aphid abundance. A possible explanation for these findings could be the availability in wheat of several aphid species early in the season that contributes to maintain and increase predator populations in wheat (Bakker 1974; Fahrig et al. 2011; Gavloski 2015b). Findings from the regression models in Chapter 3 suggest that increases in the proportion of canola in the landscape increases final aphid population size in the predator manipulation experiment. These findings are consistent with the patterns of predator movement reported in Chapter 4, with higher numbers of hover flies and green lacewings moving from soybeans to canola. The availability of food resources for aphidophagous predators in this crop, such as aphids, pollen, nectar, and extra-floral nectaries can explain this pattern of movement (Schneider 1969; McEwen et al. 2007; Bugg et al. 2008; Gavloski et al. 2011).

Altogether, my results support the hypothesis that crops in agricultural landscapes may provide essential resources for predators that are at least temporally unavailable in natural habitats. Tschardt et al. (2016) suggest this as one of five hypotheses explaining why natural habitats may fail to support biological pest control in agricultural landscapes. Characterization of landscape complexity based only on the proportion of natural habitats needs to be revised in future studies. Therefore, characterization of land-cover types into functional habitat types may help to identify their specific role supporting natural enemy abundance and diversity and pest suppression, since the larger land use categories (i.e. crops, non-crops, semi-natural habitats, etc.) may mask the actual function of small land-cover types within the larger category (Veres et al. 2013).

Directionality of predator movement does not only depend on food resources but also on non-consumptive resources such as sites for shelter, mating, nesting, reproduction and places

providing protection from disturbances and predation (Schellhorn et al. 2014). Thus, studies are required to quantify these other resources in habitats for a better understanding of the movement pattern of predators at the landscape scale. Short-term studies (such as mine) provide only a snapshot of the interactions between natural enemies and agricultural pests and provide limited insights into the role of different habitats in the landscape throughout crop growing season (Chaplin-Kramer et al. 2013; Gurr et al. 2017). Longer-term studies associating landscape complexity, predator abundance, diversity and behaviour are required to gain a better understanding on pest control services in agroecosystems and on the impacts of the changing environment as it relates to usage of pesticide, genetically modified crops and global warming on those services (Gurr et al. 2017).

My findings indicate that aphidophagous predators exert strong suppression of soybean aphid in agricultural landscapes in Manitoba. I was able to relate predator movements between soybean and adjacent habitats to the levels of pest suppression observed in soybeans, providing empirical support to the claim that landscape provided predators affect pest populations in field crops. Different crops and semi-natural land-cover types have distinct associations with pest suppression at the landscape scale, suggesting that grouping land-cover types into large categories (e.g. crop versus non-crop area) may not be appropriate for all systems or regions. Adjacent habitats and predator groups affect the directionality of the movement at the soybean field border, and soybean fields located in landscapes with nearby wheat, alfalfa, border-grass and woodland habitats may have higher levels of aphid control than those located near canola fields.

Appendix I: Localities, field area (ha) and soybean growth stages of focal soybean fields in Manitoba in 2013 and 2014.

Year	Field name	Locality	Latitude	Longitude	Field area (ha)	Soybean growth stage ¹		
						Day 0	Day 7	Day 14
2013	CA1R	Carman	49°30'03.0"N	98°01'39.6"W	0.54	V8, R3	V9, R4	V10, R4
2013	CA3	Carman	49°33'44.2"N	98°00'33.8"W	37.87	V6, R3	V8, R4	V8, R5
2013	EM1	Emerson	49°00'50.9"N	97°10'36.4"W	91.95	V7, R3	V8, R3	V8, R4
2013	EM2	Emerson	49°01'43.0"N	97°04'58.2"W	112.21	V8, R3	V7, R4	V7, R5
2013	EM3	Emerson	49°01'17.0"N	97°00'38.2"W	40.50	V7, R3	V8, R3	V8, R4
2013	GI1	Gimli	50°35'04.5"N	97°00'28.1"W	45.51	V8, R3	V9, R4	V9, R4
2013	GI5	Gimli	50°37'31.4"N	97°04'23.1"W	84.87	V7, R3	V8, R4	V8, R5
2013	GLE	Glenlea	49°38'56.9"N	97°09'17.7"W	51.47	V6, R1	V9, R3	V9, R4
2013	LB1	La Broquerie	49°33'33.4"N	96°30'29.1"W	42.03	V8, R4	V9, R4	V11, R5
2013	LB6	La Broquerie	49°34'42.5"N	96°32'43.1"W	32.94	V8, R3	V8, R4	V9, R5
2013	MO3	Morris	49°34'46.7"N	97°26'13.1"W	134.99	V7, R3	V8, R3	V8, R4
2013	RW1	Rosewood	49°47'13.9"N	96°38'21.3"W	196.06	V9, R3	V11, R4	V11, R5
2014	14CA5R	Carman	49°30'05.0"N	98°01'33.2"W	1.02	V10, R3	V9, R3	V11, R5
2014	14CA3	Carman	49°33'19.9"N	97°59'02.1"W	189.54	V7, R4	V10, R5	V11, R5
2014	14CA4	Carman	49°38'11.2"N	98°03'47.1"W	62.50	V7, R4	V8, R4	V10, R5
2014	14EL2	Elm Creek	49°41'30.5"N	97°54'58.9"W	31.85	V6, R4	V7, R4	V9, R6
2014	14GLE	Glenlea	49°38'59.9"N	97°08'59.2"W	48.18	V7, R2	V8, R4	V10, R5
2014	14LB2	La Broquerie	49°32'42.5"N	96°26'44.5"W	104.57	V6, R3	V7, R5	V9, R5
2014	14RW1	Rosewood	49°44'42.6"N	96°38'12.9"W	29.75	V7, R2.	V8, R4	V8, R4
2014	14GI3	Gimli	50°34'29.6"N	97°01'13.3"W	23.41	V8, R2	V8, R3	V10, R5
2014	14AR1	Arnes	50°49'02.5"N	97°03'04.6"W	112.67	V7, R2	V7, R4	V7, R5
2014	14WA1	Warren	50°08'40.5"N	97°31'03.5"W	111.16	V6, R4	V6, R4	V7, R5
2014	14AL1	Altona	49°07'53.4"N	97°33'53.6"W	33.95	V7, R3	V10, R5	V12, R6
2014	14LE1	Letellier	49°07'55.6"N	97°13'21.2"W	129.31	V9, R3	V11, R4	V12, R5
2014	14LE2	Letellier	49°07'55.6"N	97°18'56.1"W	60.42	V8, R3	V9, R4	V12, R5

Year	Field name	Locality	Latitude	Longitude	Field area (ha)	Soybean growth stage ¹		
						Day 0	Day 7	Day 14
2014	14EM1	Emerson	49°01'51.0"N	97°05'21.5"W	63.84	V7, R2	V7, R4	V10, R4
2014	14EM3	Emerson	49°00'50.4"N	97°09'59.2"W	81.31	V7, R3	V8, R3	V10, R5

¹ Median growth stages of soybean plants from the start of the experiment (Day 0), i.e. vegetative stage (V) and reproductive stage

(R), from visual plant counts (20 plants/field). Vegetative stages start to count from the first unifoliate leaf node as V1 and then first trifoliate leaf node or the second-node as V2, second trifoliate leaf node or the third-node as V3, and nth-node (Vn). Reproductive stages: R1 = beginning bloom, R2 = full bloom, R3 = beginning pod, R4 = full pod, R5 = beginning seed and R6 = full seed (Ritchie et al. 1985).

Appendix II: Number, mean and range percentage of different land-cover types mapped in the 27 landscapes studied in Manitoba, Canada, during field experiments in 2013 and 2014. Major land-cover types were used in multiple regression models to test their association with aphid suppression. Diversity land-cover types were used to estimate habitat diversity indices (Simpson's diversity, habitat evenness and habitat richness).

Major land-cover types	Diversity land-cover types	% area		Total polygons
		Mean ⁹	Range	
Soybean	Soybean	24.952	6.91 – 48.42	236
Cereals	Total cereals	(19.851)	2.87 – 46.99	(253)
	Wheat	17.781	2.87 – 46.99	215
	Oat	1.346	0.00 – 7.40	28
	Barley	0.724	0.00 – 6.07	10
Canola	Canola	13.227	0.00 – 36.16	146
Corn	Corn	9.957	0.00 – 36.27	111
Alfalfa	Alfalfa	7.177	0.00 – 34.63	113
Woodland ¹	Woodland	6.314	0.26 – 40.30	1399
Riparian vegetation ²	Riparian vegetation	2.784	0.00 – 11.18	138
Field border grass ³	Field border grass	2.272	0.64 – 5.04	386
Grass forage ⁴	Total of grass forage	(2.630)	0.00 – 11.21	(152)
	Brome grass	0.084	0.00 – 1.15	2
	Canary grass	0.809	0.00 – 9.94	15
	Other green grasses	1.737	0.00 – 11.21	135
Other crops ⁵	Total of other crops	(1.458)	0.00 – 14.74	(32)
	Sunflower	0.976	0.00 – 14.74	9
	Faba beans	0.114	0.00 – 3.07	1
	Pea	0.142	0.00 – 3.84	1
	Flax	0.224	0.00 – 4.38	20
	Potatoes	0.001	0.00 – 0.04	1
Pasture ⁶	Pasture	1.369	0.00 – 7.04	69
Shrubland ⁷	Shrubland	0.850	0.00 – 4.93	26
---	Marshes ⁸	0.646	0.00 – 17.18	16
---	University Farm Research plots ⁸	0.291	0.00 – 2.58	94
---	Fallow fields ⁸	0.123	0.00 – 0.84	29

Major land-cover types	Diversity land-cover types	% area		Total polygons
		Mean ⁹	Range	
---	Water bodies (lakes, reservoirs) ⁸	0.650	0.00 – 4.99	180
---	Urban (airport, town area, buildings, farm house gardens, roads, train tracks) ⁸	5.428	0.00 – 16.03	564
	Total	100.00		3,944

¹ Woodland includes trees, hedgerows and forested areas in landscape

² Riparian vegetation includes vegetation adjacent to streams, creeks, rivers, lakes and wetlands, typically less than 30 m from the water body

³ Field border grass represents strips of vegetation around fields with a mixture of grasses, broad leaf weeds, and wetland plants.

⁴ Grass forage includes brome grass (*Bromus* spp.), canary grass (*Phalaris canariensis* L.) and other green grasses harvested for animal consumption

⁵ Other crops include crops representing < 1 % of the area (except barley, which was included in cereals)

⁶ Pasture includes areas used for animal production (cattle, horse, sheep)

⁷ Shrubland represents areas with small to medium-sized woody plants (< 2.5 m in height).

⁸ Land-cover types not used in the multiple regression analysis, as they represent less than 1% of the area and are present only in a few landscapes (marshes and University farm research plots) or are not considered a source of predators.

⁹ Values between parentheses are not included in total numbers at the bottom of the table.

Appendix III: Average number of predators captured on 30 bi-directional Malaise traps, sweep-net samples and visual plant counts in 27 landscapes in Manitoba, Canada, during the two weeks of the field experiment, in 2013 and 2014.

Order: Family	Species	Individuals /bottle/day⁵	% of total	Individuals /25 sweep⁶	% of total	Individuals /plant⁷	% of total
Coleoptera: Coccinellidae ¹	Total Coccinellidae (adults)	(0.067)	(0.49)	(0.017)	(1.06)	0.004	6.82
	Larvae of Coccinellidae	-	-	0.002	0.15	0.000	0.00
	<i>Coccinella septempunctata</i> ³ Linnaeus, 1758	0.026	0.19	0.007	0.45	-	-
	<i>Harmonia axyridis</i> ³ (Pallas, 1773)	0.024	0.17	0.005	0.30	-	-
	<i>Hippodamia parenthesis</i> (Say, 1824)	0.000	0.00	0.002	0.15	-	-
	<i>Hippodamia tredecimpunctata</i> ³ (Linnaeus, 1758)	0.015	0.11	0.002	0.15	-	-
	<i>Hippodamia variegata</i> ³ (Goeze, 1777)	0.001	0.01	0.000	0.00	-	-
	<i>Chilocorus</i> sp. ³	0.001	0.01	0.000	0.00	-	-
Diptera: Syrphidae ^{1,2}	Total Syrphidae (adults)	(12.960)	(95.08)	0.580	35.63	0.006	10.23
	Total Syrphidae (larvae)	-	-	0.070	4.32	0.009	17.05
	<i>Toxomerus marginatus</i> ^{2,3} (Say, 1823)	11.085	81.33	-	-	-	-
	<i>Eupeodes latifasciatus</i> ³ (Macquart, 1829)	0.549	4.03	-	-	-	-
	<i>Eupeodes volucris</i> ³ Osten Sacken, 1877	0.536	3.93	-	-	-	-

Order: Family	Species	Individuals /bottle/day ⁵	% of total	Individuals /25 sweep ⁶	% of total	Individuals /plant ⁷	% of total
	<i>Toxomerus geminatus</i> ⁴ (Say, 1823)	0.259	1.90	-	-	-	-
	<i>Sphaerophoria contigua</i> ⁴ Macquart, 1847	0.110	0.81	-	-	-	-
	<i>Platycheirus hyperboreus</i> ³ (Staeger, 1845)	0.081	0.59	-	-	-	-
	<i>Sphaerophoria philanthus</i> ³ Meigen	0.069	0.51	-	-	-	-
	<i>Platycheirus nearcticus</i> ⁴ Vockeroth, 1986	0.041	0.30	-	-	-	-
	<i>Syrphus rectus</i> ³ Osten Sacken, 1875	0.036	0.26	-	-	-	-
	<i>Parhelophilus laetus</i> ⁴ (Loew, 1963)	0.034	0.25	-	-	-	-
	<i>Eumerus strigatus</i> ⁴ (Fallen, 1817)	0.032	0.23	-	-	-	-
	<i>Eupeodes americanus</i> ³ (Wiedemann, 1830)	0.026	0.19	-	-	-	-
	<i>Allograpta obliqua</i> ³ (Say, 1823)	0.024	0.17	-	-	-	-
	<i>Syritta pipiens</i> ⁴ (Linnaeus, 1758)	0.024	0.17	-	-	-	-
	<i>Platycheirus immarginatus</i> ³ (Zetterstedt, 1849)	0.021	0.16	-	-	-	-
	<i>Eupeodes (Lapposyrphus)</i> <i>lapponicus</i> ⁴ (Zetterstedt, 1838)	0.012	0.09	-	-	-	-
	<i>Melanostoma mellinum</i> ³ (Linnaeus, 1758)	0.004	0.03	-	-	-	-

Order: Family	Species	Individuals /bottle/day ⁵	% of total	Individuals /25 sweep ⁶	% of total	Individuals /plant ⁷	% of total
	<i>Syrphus ribesii</i> ³ (Linnaeus, 1758)	0.003	0.03	-	-	-	-
	<i>Chrysotoxum derivatum</i> ⁴ Walker, 1849	0.003	0.03	-	-	-	-
	<i>Ocyptamus fuscipennis</i> ³ (Macquart, 1834)	0.002	0.02	-	-	-	-
	<i>Paragus haemorrhous</i> ³ Meigen, 1822	0.001	0.01	-	-	-	-
	<i>Platycheirus granditarsis</i> ⁴ (Forster, 1771)	0.001	0.01	-	-	-	-
	<i>Ferdinandea buccata</i> ⁴ (Loew, 1863)	0.001	0.01	-	-	-	-
	<i>Lejops (Eurimyia) lineatus</i> ⁴ (Fabricius, 1787)	0.001	0.01	-	-	-	-
	<i>Helophilus fasciatus</i> ⁴ Walker, 1849	0.001	0.01	-	-	-	-
	<i>Neocnemodon</i> sp. ⁴	0.001	0.01	-	-	-	-
Hemiptera: Anthocoridae ¹	<i>Orius insidiosus</i> ³ (Say, 1832) (adults)	0.261	1.92	0.553	33.97	0.018	32.95
	<i>O. insidiosus</i> (nymphs)	-	-	0.230	14.10	0.014	25.00
Nabidae ¹	Damsel bugs (adults)	0.005	0.03	0.030	1.82	0.000	0.00
	Damsel bugs (nymphs)	-	-	0.044	2.73	0.000	0.00
Neuroptera: Chrysopidae ^{1,2}	Total green lacewings (adults)	(0.297)	(2.18)	(0.057)	(3.50)	0.004	6.82
	Total green lacewings (larvae)	-	-	0.035	2.12	0.001	1.14
	<i>Chrysoperla</i> spp. ⁸	0.196	1.44	0.012	0.76	-	-

Order: Family	Species	Individuals /bottle/day ⁵	% of total	Individuals /25 sweep ⁶	% of total	Individuals /plant ⁷	% of total
	<i>Chrysoperla carnea</i> ³ (Stephens, 1836)	0.060	0.44	0.020	1.21	-	-
	<i>Chrysopa</i> spp. ³	0.039	0.29	0.025	1.52	-	-
	<i>Ceraeochrysa lineaticornis</i> ⁴ (Fitch, 1855)	0.001	0.01	0.000	0.00	-	-
Hemerobiidae ¹	Brown lacewings (adults)	0.040	0.30	0.000	0.00	0.000	0.000
	Brown lacewings (larvae)	-	-	0.010	0.61	0.000	0.000
	Total	13.630	100	1.628	100	0.054	100

¹ Higher taxonomic levels of aphidophagous predators used in multiple regression models to examine their association with aphid suppression.

² Numbers of *T. marginatus*, *C. carnea* and *Chrysopa* spp., were used for multiple regression models.

³ Aphidophagous predators captured in bi-directional Malaise traps.

⁴ Non-aphidophagous insects captured in bi-directional Malaise traps (these species were not used for multiple regression models).

⁵ Number of individuals captured during the first two weeks of the study was standardized to 1-day captures since 8-day rather than 7-day sampling periods occurred in some fields due to rain (n = 3).

⁶ Average number of individuals captured in sweep-net samples during the three sampling periods.

⁷ Average number of observed individuals in visual soybean plant counts during the three sampling periods.

⁸ Not included in multiple regression models as it was not possible to identify to species level.

Values between parentheses are not included in total numbers at the bottom of the table.

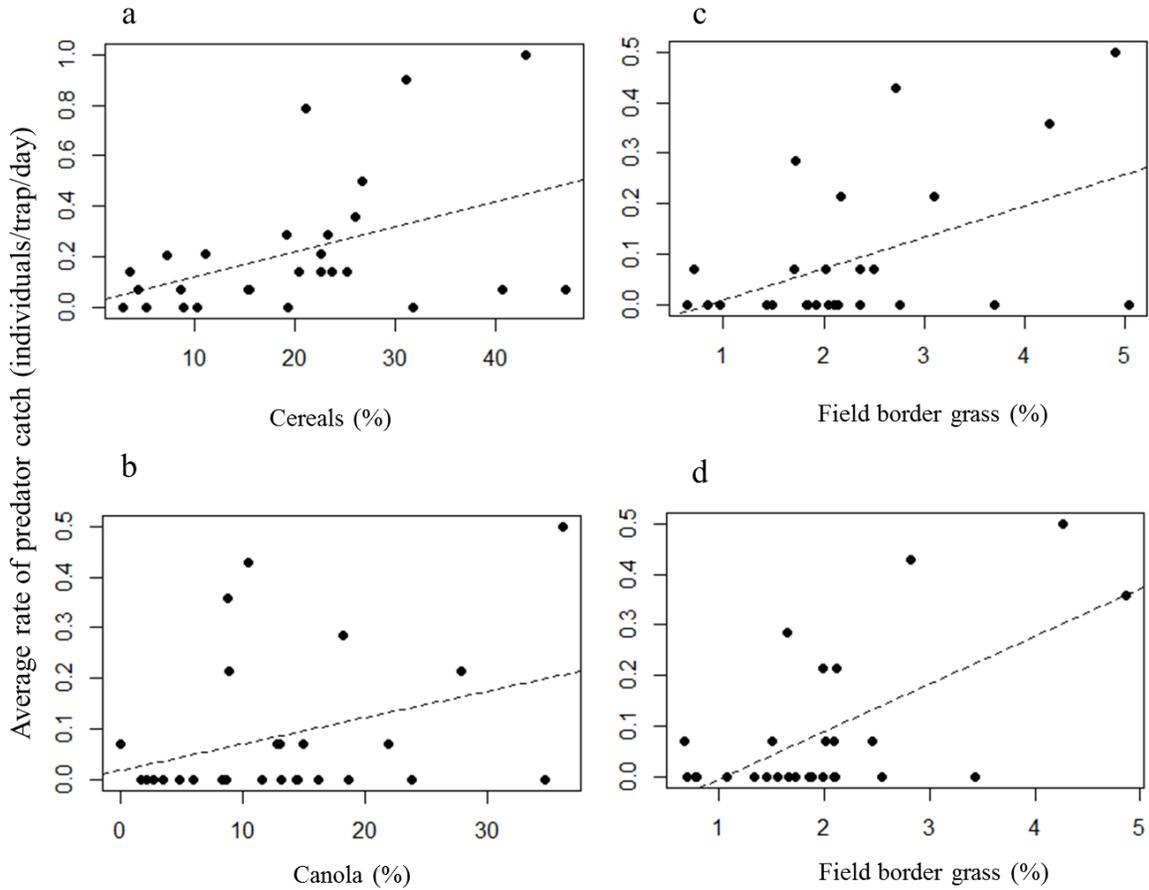
Appendix IV: Summary statistics of multiple regression models assessing the relationship between final population size of soybean aphids exposed to predation in the open treatment and landscape variables (landscape models), levels of aphidophagous predator movement (predator models) and both sets of variables combined (landscape + predator models) at different spatial scales in Manitoba.

Scale (km)	Models	Log-likelihood	AIC _c	Δi	w_i	Adj. r^2	P value	Partial correlation with dependent variable
Null model								
	I + A	-30.69	68.43	4.37	0.03	0.52	< 0.0001	
Landscape models								
2.0	I + A**** - CE* + CA	-25.60	64.06	0.00	0.29	0.64	< 0.0001	A (0.65), CE (-0.40), CA (0.05); Moran's $I = -0.25, p = 0.11$
0.5	I + A**** + W* + CA**	-26.06	64.97	0.91	0.18	0.63	< 0.0001	A (0.56), W (0.43), CA (0.48)
1.5	I + A**** - CE*	-27.84	65.49	1.43	0.14	0.59	< 0.0001	A (0.67), CE (-0.38)
0.25	I + A**** + W** + CA**	-26.79	66.43	2.37	0.09	0.61	< 0.0001	A (0.56), W (0.48), CA (0.56)
0.5	I + A**** + BG	-28.90	67.61	3.55	0.05	0.56	< 0.0001	A (0.67), BG (0.17)
1.0	I + A**** + CA	-29.14	68.09	4.03	0.04	0.55	< 0.0001	A (0.60), CA (0.16)
1.0	I + A**** - CE	-29.19	68.20	4.14	0.04	0.55	< 0.0001	A (0.66), CE (-0.26)
0.5	I + A**** - SB - CE	-27.67	68.20	4.14	0.04	0.58	< 0.0001	A (0.59), SB (-0.04), CE (-0.16)
1.5	I + A**** + CA	-29.30	68.42	4.36	0.03	0.55	< 0.0001	A (0.59), CA (0.10)
0.25	I + A**** + BG	-29.61	69.04	4.98	0.02	0.53	< 0.0001	A (0.66), BG (0.13)
1.0	I + A**** + W - SH	-28.21	69.27	5.21	0.02	0.56	< 0.0001	A (0.62), W (0.21), SH (-0.20)
0.25	I + A**** - SB - CE	-28.63	70.11	6.06	0.01	0.55	< 0.0001	A (0.56), SB (-0.10), CE (-

Scale (km)	Models	Log-likelihood	AIC _c	Δi	w_i	Adj. r^2	P value	Partial correlation with dependent variable
1.5	I + A*** + W - SH	-28.94	70.74	6.68	0.01	0.54	< 0.0001	0.12) A (0.59), W (0.23), SH (-0.16)
Predator models								
	I + A*** - gl** + bl	-24.99	62.83	0.00	0.64	0.66	< 0.0001	A (0.68), gl (-0.52), bl (0.26); Moran's $I = 0.28$, $p = 0.02$
	I + A*** - gl**	-27.22	64.26	1.43	0.31	0.61	< 0.0001	A (0.74), gl (-0.51)
	I + A*** - co*	-29.12	68.06	5.23	0.05	0.55	< 0.0001	A (0.74), co (-0.37)
Landscape + predator models								
0.5	I + A*** - gl** + CA + BG**	-23.57	63.34	0.00	0.24	0.68	< 0.0001	A (0.77), gl (-0.52), CA (0.34), BG (0.18); Moran's $I = -0.14$, $p = 0.45$
0.25	I + A*** - gl** + CA* + BG	-23.98	64.17	0.83	0.16	0.67	< 0.0001	A (0.76), gl (-0.54), CA (0.39), BG (0.10)
1.5	I + A*** - gl*** - SH*	-25.66	64.19	0.85	0.15	0.64	< 0.0001	A (0.73), gl (-0.58), SH (-0.38)
1.0	I + A*** - gl** + CA	-25.84	64.54	1.20	0.13	0.63	< 0.0001	A (0.73), gl (-0.50), CA (0.25)
2.0	I + A*** - co- CE* + bl	-24.44	65.08	1.74	0.10	0.65	< 0.0001	A (0.73), co (-0.37), CE (-0.46), bl (0.17)
1.5	I + A*** - co [†] - CE*	-26.30	65.46	2.12	0.08	0.62	< 0.0001	A (0.78), co (-0.37), CE (-0.42)
1.0	I + A*** + bl + W	-27.15	67.15	3.81	0.04	0.60	< 0.0001	A (0.63), bl (0.29), W (0.36)
0.5	I + A*** - co* - CE	-27.19	67.23	3.90	0.03	0.59	< 0.0001	A (0.74), co (-0.38), CE (-0.29)
1.5	I + A*** + bl + W	-27.37	67.61	4.27	0.03	0.59	< 0.0001	A (0.63), bl (0.31), W (0.35)
0.25	I + A*** + bl + W	-27.59	68.04	4.70	0.02	0.58	< 0.0001	A (0.63), bl (0.27), W (0.35)
1.0	I + A*** - co [†] - CE - SH	-26.24	68.68	5.35	0.02	0.60	< 0.0001	A (0.79), co (-0.37), CE (-

Scale (km)	Models	Log-likelihood	AIC _c	Δi	w_i	Adj. r^2	P value	Partial correlation with dependent variable
0.25	I + A*** - co - CE - SB*	-27.35	70.90	7.56	0.01	0.57	0.0001	0.29), SH (-0.29) A (0.66), co (-0.33), CE (-0.23), SB (-0.42)

Notes: Model terms include intercept (I); aphid potential growth estimated using final aphid population size in predator exclusion cages (A); landscape variables: total proportion of field border grass (BG), cereals (CE), canola (CA), woodland (W), soybean (SB), shrubland (SH); and predator movement variables: average daily catch in bi-directional Malaise traps of aphidophagous green lacewings (gl), brown lacewings (bl) and lady beetles (co) during two weeks. Adjusted (Adj.) r^2 is shown. In all models, the natural log of the average final aphid population size in the open treatment in each field was the dependent variable. For each type of model, the model presented first and in bold was the most supported by the data (smallest AIC_c); also shown are competing models with substantial support in each of the three model groups ($\Delta i < 2$). Akaike weight (w_i) indicates the support of each model within a group of models. Tests of autocorrelation values for the residuals for the three most supported models are shown using Moran's I with statistics. (\dagger $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)



Appendix V: Correlation between average rate of predator captures in bi-directional Malaise traps (14 days of capture, $n = 27$ landscapes during 2013 and 2014) and proportion of land-cover types. (a) Catch of *Chrysoperla carnea* and *Chrysopa sp.* vs total proportion of cereals within a spatial scale of 2 km, (b) catch of brown lacewings vs proportion of canola within 1.5 km, (c) catch of brown lacewings vs total proportion of field border grass within 2 km and (d) within 1.5 km. A dashed line within correlation plot shows the linear trend between two variables.

Appendix VI: Summary of border types selected for bi-directional Malaise traps in 2013 and 2014.

Border type	Treatment code	2013 ¹		2014 ²		Total number of bottles
		Number of traps	Number of bottles	Number of traps	Number of bottles	
Alfalfa/Soybean	alfalfa to soybean	4	12	3	12	24
	soybean to alfalfa		12		12	24
Canola/Soybean	canola to soybean	3	9	4	16	25
	soybean to canola		9		16	25
Grass/Soybean	grass to soybean	1	3	1	4	7
	soybean to grass		3		4	7
Woodland/Soybean	woodland to soybean	5	15	6	24	39
	soybean to woodland		15		24	39
Wheat/Soybean	wheat to soybean	1	3	2	8	11
	soybean to wheat		3		8	11
Soybean/Soybean	Control to field interior	-	-	8	32	32
	Control to field margin	-	-		32	32
Total		14	84	24	192	276

¹3 weeks sampled in 2013

²4 weeks sampled in 2014

Appendix VII: Average number of predators (standardized per day) captured on 38 bi-directional Malaise traps (14 traps in 2013 and 24 in 2014) in Manitoba, Canada, for 3 weeks in 2013 and 4 weeks in 2014 (n = 276).

Order	Family	Species	Individuals/bottle/day ⁵	% of total
Coleoptera	Coccinellidae ¹		(0.173)	(1.273)
		<i>Coccinella septempunctata</i> ³ Linnaeus, 1758	0.104	0.765
		<i>Hippodamia tredecimpunctata</i> ³ (Linnaeus, 1758)	0.041	0.300
		<i>Harmonia axyridis</i> ³ (Pallas, 1773)	0.024	0.174
		<i>Hippodamia variegata</i> ³ (Goeze, 1777)	0.002	0.015
		<i>Psyllobora vigintimaculata</i> ³ (Say, 1824)	0.001	0.008
		<i>Chilocorus</i> sp. ³	0.001	0.007
		<i>Hyperaspis conviva</i> ³ Casey, 1924	0.001	0.004
Diptera	Syrphidae ¹		(12.525)	(92.077)
		Aphidophagous hover flies ²	(12.209)	(89.752)
		<i>Toxomerus marginatus</i> ³ (Say, 1823)	11.543	84.857
		<i>Eupeodes latifasciatus</i> ³ (Macquart, 1829)	0.264	1.937
		<i>Eupeodes volucris</i> ³ Osten Sacken, 1877	0.251	1.844
		<i>Toxomerus geminatus</i> ⁴ (Say, 1823)	0.163	1.197
		<i>Sphaerophoria contigua</i> ⁴ Macquart, 1847	0.073	0.539
		<i>Sphaerophoria philanthus</i> ³ Meigen	0.052	0.384
		<i>Platycheirus hyperboreus</i> ³ (Staeger, 1845)	0.042	0.312
		<i>Platycheirus nearcticus</i> ⁴ Vockeroth, 1986	0.021	0.155
		<i>Parhelophilus laetus</i> ⁴ (Loew, 1963)	0.018	0.001
		<i>Syrphus rectus</i> ³ Osten Sacken, 1875	0.018	0.133
		<i>Syritta pipiens</i> ⁴ (Linnaeus, 1758)	0.015	0.110
		<i>Eumerus strigatus</i> ⁴ (Fallen, 1817)	0.014	0.102
		<i>Eupeodes americanus</i> ³ (Wiedemann, 1830)	0.013	0.099
		<i>Allograpta obliqua</i> ³ (Say, 1823)	0.010	0.076
		<i>Platycheirus immarginatus</i> ³ (Zetterstedt, 1849)	0.009	0.068
		<i>Eupeodes (Lapposyrphus) lapponicus</i> ⁴ (Zetterstedt, 1838)	0.005	0.038

Order	Family	Species	Individuals/bottle/day ⁵	% of total
		<i>Chrysotoxum derivatum</i> ⁴ Walker, 1849	0.004	0.026
		<i>Syrphus ribesii</i> ³ (Linnaeus, 1758)	0.002	0.015
		<i>Melanostoma mellinum</i> ³ (Linnaeus, 1758)	0.002	0.011
		<i>Ocyptamus fuscipennis</i> ³ (Macquart, 1834)	0.001	0.008
		<i>Paragus haemorrhous</i> ³ Meigen, 1822	0.001	0.008
		<i>Neocnemodon</i> sp. ⁴	0.001	0.007
		<i>Platycheirus granditarsis</i> ⁴ (Forster, 1771)	0.001	0.004
		<i>Ferdinanda buccata</i> ⁴ (Loew, 1863)	0.001	0.004
		<i>Lejops (Eurimyia) lineatus</i> ⁴ (Fabricius, 1787)	0.001	0.004
		<i>Helophilus fasciatus</i> ⁴ Walker, 1849	0.001	0.004
Hemiptera	Anthocoridae ¹	<i>Orius insidiosus</i> ³ (Say, 1832)	0.621	4.564
	Nabidae ¹	[Damsel Bugs] ³	0.005	0.038
Neuroptera	Chrysopidae ¹	Aphidophagous green lacewings ²	(0.199)	(1.465)
		<i>Chrysoperla carnea</i> ³ (Stephens, 1836)	(0.087)	(0.641)
		<i>Chrysopa</i> sp. ³	0.063	0.463
		<i>Chrysoperla</i> spp. ⁶	0.024	0.178
		<i>Ceraeochrysa lineaticornis</i> ⁴ (Fitch, 1855)	0.111	0.817
	Hemerobiidae ¹	[Brown Lacewings]	0.001	0.008
			0.079	0.582
Total			13.603	100

¹ Higher taxonomic levels of aphidophagous predators used for analysis of immigration and emigration.

² Abundances of aphidophagous species in Syrphidae and Chrysopidae families were used for analysis of immigration and emigration.

³ Aphidophagous predators captured in bi-directional Malaise traps.

⁴ Non-aphidophagous insects captured in bi-directional Malaise trap (not used for statistical analysis).

⁵ Average number of individuals adjusted to 1-day intervals, as 8-day intervals due to rain occurred in some fields.

⁶ Not included in multiple regression models as it was not possible to identify to species level.

Values between parentheses are not included in total numbers at the bottom of the table.

Appendix VIII: Observations of canola flowering in canola fields adjacent to soybean fields.

Year	Name of soybean field adjacent to a canola field	Locality	Latitude	Longitude	Canola flowering			
					week 1	week 2	week 3	week 4
2013	MO3	Morris	49°34'46.7"N	97°26'13.1"W	starts to bloom	in bloom	full bloom	-
	LB1	La Broquerie	49°33'33.4"N	96°30'29.1"W	flowering	full bloom	less flowers in the field	-
	GI5	Gimli	50°37'31.4"N	97°04'23.1"W	starts to bloom	in bloom	full bloom	-
2014	14EL2	Elm Creek	49°41'30.5"N	97°54'58.9"W	in bloom	full bloom	less flowers in the field	no flowers
	14AL1	Altona	49°07'53.4"N	97°33'53.6"W	starts to bloom	in bloom	full bloom	less flowers in the field
	14EM1	Emerson	49°01'51.0"N	97°05'21.5"W	in bloom	full bloom	less flowers in the field	no flowers
	14RW1	Rosewood	49°44'42.6"N	96°38'12.9"W	full bloom	less flowers in the field	no flowers	no flowers

Appendix IX: Assessment of the effects of paint markings and storage temperature on *C. septempunctata* viability for MRR experiments.

Laboratory experiments were carried out 1) to determine the survival of seven-spotted lady beetles at 5 °C, 2) to assess if marking paints have negative impacts on lady beetles and 3) to evaluate the time that markings remain on the elytra. Seven-spotted lady beetles were stored in 12 ventilated containers (11.5 cm diameter ×14 cm height, Bug Tub Inc., Lacombe, AB, Canada) (five beetles/container) at two different temperatures for a week. Six ventilated containers with beetles were stored in the growth room at 5 °C and other six containers were stored at 23 °C in a laboratory as controls. Relative humidity (RH) inside the containers ranged from 40 – 55 % at both temperatures. Both temperature and RH were measured using a HOBO® H8 RH/Temp/Light External Logger (Onset, Bourne, MA, USA). Survival of lady beetles was monitored daily during the experimental period. After seven days, all surviving beetles were marked with paint markers as described in the methods of chapter 4. Then they were stored at the same temperatures as they were previously stored for the next two weeks. Survival of lady beetles and any visual degradation of painted spots were checked daily. Water was supplied in a small container inside the larger ventilated container. All lady beetles survived and were immobilized at 5 °C during the first week. After marking them, all paint markings were retained on their elytra for two weeks at 5 °C. However, 22 out of 30 beetles started to lose their paint markings after six days from the marking date at 23 °C. All paint markings disappeared after ten days at 23 °C. All 60 lady beetles survived after marking them at 5 °C and 23 °C for two weeks. I concluded that the marking procedure, and storage temperatures at 5 °C and 23 °C were not deleterious for seven-spotted lady beetles and can be used for field experiment. In addition,

recaptures should be done within 5 days after marking lady beetles, as the paints are starting to disappear from them after 6 days.

Appendix X: Weather condition during the mark-release-recapture experiments carried out in soybean and alfalfa fields located in Gimli and Carman, Manitoba, in 2013 and 2014, respectively.

Weather parameters	Gimli			Carman		
	July 10, 2013	July 11, 2013	July 12, 2013	July 23, 2014	July 24, 2015	July 25, 2014
Minimum Temperature ¹	5.8 °C	6.5 °C	16.2 °C	9.3 °C	9.3 °C	15.3 °C
Mean Temperature ¹	15.9 °C	13.7 °C	19.0 °C	16.1 °C	15.7 °C	21.1 °C
Maximum Temperature ¹	25.1 °C	25.6 °C	25.7 °C	24.4 °C	23.7 °C	26.9 °C
Mean Dew Point ¹	7.4 °C	8.9 °C	16.4 °C	12.6 °C	13.2 °C	15.8 °C
Total Precipitation ²	0.00 mm	8.60 mm	21.5 mm*	0.00 mm	0.00 mm	0.00 mm
Mean Wind Speed ¹	5.37 km/h	8.70 km/h	4.82 km/h	5.93 km/h	6.85 km/h	13.70 km/h
Wind direction ²	morning (West to East), afternoon (South West to North East)	morning (South West to North East), afternoon (West to East)	(West to East)	(West to East)	morning (North West to South East), afternoon (West to East)	morning (West to East), afternoon (South West to North East)
Wind direction through fields	alfalfa to soybean	alfalfa to soybean	alfalfa to soybean	alfalfa to soybean	alfalfa to soybean	alfalfa to soybean

Weather parameters obtained from the nearest weather stations to sampling fields (i.e. Gimli Industrial Park Airport Weather Station and University of Manitoba Carman Weather Station):

¹<http://www.almanac.com/weather/history/MB>

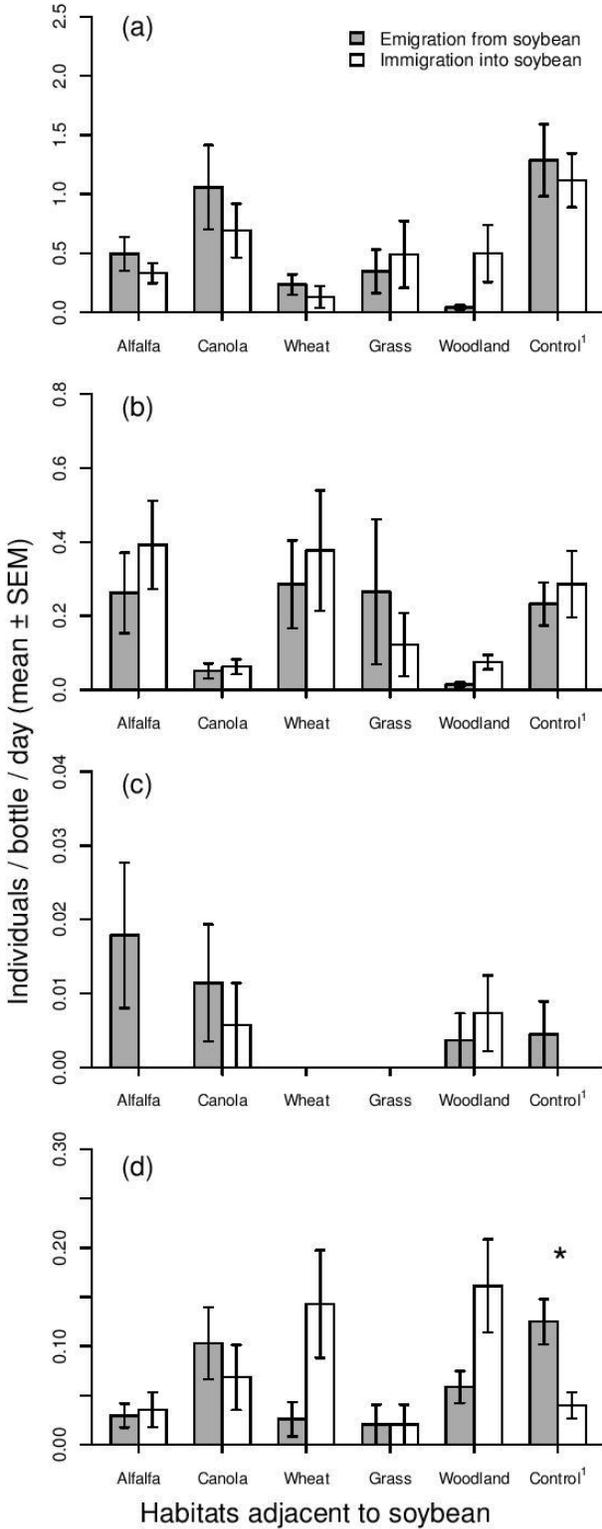
²<http://www.theweathernetwork.com/ca>

*Rain occurred after last sampling

Appendix XI: Statistics of Kruskal-Wallis pairwise comparisons adjusted by sequential Bonferroni for captures of marked lady beetles in sweep-net samples in 2013 and 2014. (* indicates significant comparisons at a global $\alpha = 0.05$)

Year	Comparisons	Kruskal-Wallis chi-squared	<i>df</i>	Bonferroni adjusted α-value	Kruskal-Wallis <i>p</i>-value
2013	alf-alf vs alf-sb	13.65	1	0.0083	0.0002*
	alf-sb vs sb-sb	8.68	1	0.0100	0.0032*
	alf-alf vs sb-alf	7.07	1	0.0125	0.0079*
	alf-sb vs sb-alf	3.07	1	0.0167	0.0797
	sb-alf vs sb-sb	2.92	1	0.0250	0.0877
	alf-alf vs sb-sb	0.80	1	0.0500	0.3716
2014	alf-sb vs sb-alf	8.44	1	0.0083	0.0037*
	alf-alf vs alf-sb	4.57	1	0.0100	0.0326
	sb-alf vs sb-sb	3.55	1	0.0125	0.0595
	alf-alf vs sb-sb	1.20	1	0.0167	0.2739
	alf-sb vs sb-sb	0.92	1	0.0250	0.3385
	alf-alf vs sb-alf	0.78	1	0.0500	0.3781

Appendix XII: Captures of aphidophagous predators showing movement trends between soybean and adjacent habitats.



Average daily emigration and immigration of (a) minute pirate bugs, (b) lady beetles, (c) damsel bugs, and (d) brown lacewings between soybean and different adjacent habitats, combining two years of sampling (7 weeks in total). Sampling consisted of bi-directional Malaise traps established on five adjacent habitats: soybean-alfalfa (n= 24 bottles), soybean-canola (n= 25), soybean-grass (n=7), soybean-woodland (n=39), soybean-wheat (n=11) and control (soybean fields, 100 m from the field border, n=32; see Appendix VI). Significant differences ($p < 0.05$) between emigration and immigration are indicated by *. ¹Control bi-directional Malaise traps setup in a subset of fields in 2014 (n=8 fields).

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