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LANDSCAPE SCALE AND WITHIN-FIELD INFLUENCES ON
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IN SOYBEAN FIELDS.

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# LANDSCAPE SCALE AND WITHIN-FIELD INFLUENCES ON PREDATOR ABUNDANCE AND BIOCONTROL SERVICES IN SOYBEAN FIELDS.

By

Mary Margaret Gardiner

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# ABSTRACT

# LANDSCAPE SCALE AND WITHIN-FIELD INFLUENCES ON PREDATOR ABUNDANCE AND BIOCONTROL SERVICES IN SOYBEAN FIELDS.

By

Mary Margaret Gardiner

The soybean aphid, *Aphis glycines* Matumura, is an invasive species first detected in the U.S. in 2000. This pest has now spread throughout soybean growing regions of the U.S. and Canada. Previous work has demonstrated that natural enemies are key drivers of soybean aphid population dynamics within soybean fields. The objectives of my dissertation research were to investigate how landscape diversity and composition influenced the species pool of potential biocontrol agents supplied to soybean fields and determine how within-field interactions between these species affected net biocontrol services. I investigated these objectives in replicate sites across Iowa, Michigan, Minnesota, and Wisconsin from 2005-2007. I measured the impact of predators by experimentally excluding or allowing access to soybean aphid infested plants and comparing aphid population growth over 14 d. I found that while predators significantly suppressed soybean aphid across the region, there was a great deal of site to site variation. To determine how the amount of biocontrol services supplied to a soybean field was influenced by the surrounding landscape, I calculated a biological control services index (BSI) based on relative suppression of aphid populations and related it to landscape diversity and composition at multiple spatial scales surrounding each site. BSI values increased with landscape diversity, measured as Simpson's D. Landscapes dominated by corn and soybean fields provided less biocontrol service to soybean compared with landscapes with an abundance of crop and non-crop habitats.

The distribution and abundance of natural and agricultural habitats within the landscape also greatly influenced the abundance of key predator species including Coccinellidae, Carabidae, and Araneae. I found variation in the response to landscape variables of the study organisms based on their trophic level, phenology, and whether they were native to the north-central U.S. The activity density of Araneae increased in soybean fields in landscapes with an abundance of forests and grasslands. Relationships with Carabidae activity density varied, with adult-overwintering and predatory species increasing and larval-overwintering species declining with the abundance of grassland in the landscape. The coccinellid community also exhibited varied responses to landscape diversity and composition. Native coccinellids were most abundant in low-diversity landscapes with an abundance of grassland habitat while exotic coccinellid increased with the abundance of forested habitats.

I also investigated how within-field intraguild interactions affected species abundance and biocontrol services in soybean fields. I found that *H. axyridis* was a significant intraguild predator of both *Aphidoletes aphidimyza* and *Chrysoperla carnea,* however, the direct impact of *H. axyridis* on *A. glycines* overcame these negative impacts on overall biocontrol. I also measured the extent of IGP of native coccinellid eggs in soybean fields. I found significant IGP occurred and the composition of the potential egg predators varied by state. In Michigan, exotic coccinellids were the most abundant predators while in Iowa native species including *C. maculata*, *Hippodamia parenthesis*, and *Collops nigriceps* dominated the predator community. Thus, in Michigan landscapes, consumption of native coccinellid eggs favors exotic coccinellids while in Iowa, this resource is more likely to sustain other native species.

For Steve

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# KEY TO SYMBOLS OR ABBREVATIONS

| | |
|---|---|
| AICc | Akaike's Information Criterion, adjusted for small sample size |
| BSI | Biocontrol Services Index |
| cm | Centimeters |
| D | Simpson's Diversity |
| F | Fisher distribution |
| h | Hours |
| IGP | Intraguild predation |
| $K_i$ | Number of parameters in model |
| m | Meters |
| mm | Millimeters |
| n | Number of observations |
| $P$ | Probability under the assumption that the null hypothesis is true |
| PC1 | Principal component 1 |
| PC2 | Principal component 2 |
| $r^2$ | Coefficient of determination |
| SEM | Standard error of the mean |
| Spp. | Species |
| $W_i$ | Akaike weight |
| $\Delta_i$ | AICc differences |

# CHAPTER 1

# INFLUENCE OF LANDSCAPE AND WITHIN-FIELD INTERACTIONS ON ARTHROPOD FOOD WEBS IN AGROECOSYSTEMS.

## Introduction

Food webs are commonly used to depict feeding relationships within ecological communities. However, in agroecosystems, knowledge of food web interactions is often limited, due to the complexity of tri-trophic relationships and the number of species involved (Bascompte and Melian 2005). In addition, organisms that comprise agricultural food webs live in a spatially heterogeneous world, where the within-field community is variously connected to the surrounding landscape (Thompson and Townsend 2003). The arthropod components of food webs are likely to cross spatial boundaries to arrive in crop fields from other areas that provide alternative prey or overwintering habitat. Therefore, landscape variables such as habitat complexity, quality, and patchiness as well as an organism's perceived spatial scale can all impact the structure and function of agricultural food webs.

Invasions of exotic species are likely to profoundly affect the structure of food webs in agroecosystems. In many cases, biological invasions extend beyond the introduction of single species, sometimes involving the transplantation of an entire exotic landscape (Thompson and Townsend 2003). The latter appears to be true in the case of the soybean aphid, its host plants, and natural enemies. The soybean aphid *Aphis glycines* Matsumura, a native of Asia, was first detected in the US in Wisconsin in July of 2000. The distribution of soybean aphid now extends throughout the north-central soybean growing states and into Canada. In the soybean system, species occupying each trophic level of the food web are introduced into the north-central U.S. Both the primary and secondary host plants, common buckthorn, *Rhamnus cathartica* L. (Rhamnaceae) and the cultivated soybean, *Glycine max L.* (Fabaceae), the soybean aphid, and a complex lady beetle predators, *Harmomia axyridis* Pallas, *Coccinella septumpuncata* L., *Hippodamia variegata* (Goeze), and *Propylea quatuordecimpunctata* (L.) (Coccinellidae) are non-native species. These non-native organisms also interact with a host of native species including *Chrysoperla carnea* (Stephens) (Chrysopidae), *Aphidoletes aphidomyza* (Rondani) (Cecidomyiidae), *Hippodamia convergens* Guérin-Méneville (Coccinellidae), *Coleomegilla maculata* DeGeer (Coccinellidae), and *Orius insidiosus* Say (Hemiptera).

Studying how landscape variables across the north-central U.S. affect the functioning of this food web provids a model system to investigate landscape mediated predator-predator and predator-prey dynamics. Soybean fields are ephemeral habitats where disturbances such as tillage, pesticide application, and harvesting require repeated re-colonization by soybean aphid and its natural enemies. Landscape elements act as both a source and a sink for these species, shaping within-field interactions of soybean aphid and its natural enemies. In this dissertation, I began by investigating the role *H. axyridis* plays in the biological control of soybean aphid (Chapter 2). I was interested in determining whether early season intraguild predation of the native larval predator community by this exotic coccinellid resulted in a release of *A. glycines*. I followed this study of within-field dynamics by determining how the landscape surrounding soybean fields influenced biocontrol services at a regional scale, studying the suppression of *A. glycines* supplied by predators in fields across Iowa, Michigan, Minnesota, and

Wisconsin (Chapter 3). Next, I examined the influence of landscape composition on two natural enemy guilds: ground-dwelling species and native and exotic coccinellids (Chapters 4 and 5). Chapter 4 examined the influence of landscape composition on the activity density of Araneae and Carabidae in soybean fields. I was specifically interested in how dispersal capacity, trophic status, and overwintering stage of these species affected their response to landscape variables. In Chapter 5, I examined the relationship between the abundance of native and exotic Coccinellidae in soybean fields and the surrounding landscape. Specifically, I was interested in determining if landscape variables such as the amount of semi-natural habitat present facilitated the success of exotic populations. Finally, I connect landscape to within-field interactions to examine how the landscape around soybean fields influences intraguild predation of native coccinellids by exotics (Chapter 6). Herein, I review soybean aphid biology, known natural enemies, potential within-field interactions, and landscape dynamics.

## Biology of the soybean aphid

*Aphis glycines* exhibits a heteroecious holocyclic lifecycle (Ragsdale et al. 2004). From late spring to early fall, soybean aphid feeds and reproduces viviparously on soybean. Many generations of alate and apterous aphids can occur during the growing season. In the fall, reduced temperature and photoperiod influence the production of winged males and female gynoparae that emigrate in search of *Rhamnus* hosts. Several species of *Rhamnus* are present within the invasive range of this pest. Yoo et al. (2005) compared six species of *Rhamnus* and found that gynoparae prefer *R. cathartica* and *R. alnifolia* L'Her, over *R. caroliniana* Walter, *R. frangula* L., *R. frangula* 'Asplenifolia', or *R. frangula* 'Columnaris'. Gynoparae exhibited greater longevity and reproduction on *R.*

*cathartica* and *R. alnifolia,* and oviparous nymphs produced by gynoparae survived to maturity only on these hosts. These oviparae will lay the overwintering eggs. In the spring soybean aphids emerge from eggs and produce two generations on *Rhamnus* consisting primarily of wingless females. A third generation of alate aphids leaves the overwintering host searching for soybean (Ragsdale et al. 2004).

Temperature is a key regulator of soybean aphid population dynamics. McCornack et al. (2004) reported that 25°C was the optimal developmental threshold for *A. glycines*. At higher temperatures, net fecundity, gross fecundity, generation time, and life expectancy are decreased. Reproductive periods vary with temperature; aphids reproduce longer and have more offspring at 20° and 25°C than at 30°C and do not survive above 34.9°C (McCornack et al. 2004).

The paths of soybean aphid colonization of soybean produces a highly patchy distribution. Newly arrived females give birth to produce small colonies on scattered plants within a field. When soybean is in the vegetative growth stage, *A. glycines* can typically be found on partially expanded trifoliates, petioles and stems (Ragsdale et al. 2004). When the plant begins to flower, set pods and develop lateral branches, aphids become widely dispersed on the plant (Ragsdale et al. 2004). When soybean enters reproductive growth, its nutritional quality for the aphid changes, aphids on lower, mature leaves can appear pale and smaller than aphids found feeding on the growing points in pre-reproductive plants (Ragsdale et al. 2004).

### Impacts of soybean aphid

Feeding by *A. glycines* on the leaves, stems, and pods of the soybean plant causes reductions in photosynthetic rate, plant growth, and seed yield of soybean plants

(DiFonzo and Hines 2002). This pest can also vector several viruses, including alfalfa mosaic, soybean dwarf, soybean stunt, soybean mosaic, tobacco ringspot, and bean yellow mosaic (Clark and Perry 2002, Wang and Ghabrial 2002). Honeydew production by the soybean aphid promotes the growth of sooty molds further reducing the photosynthetic capacity of the soybean plant (Hirano et al. 1996). To prevent economic losses from soybean aphid damage, U.S. growers may make multiple insecticide applications per year. In 2003, over 42 million acres of soybean in the north-central U.S. were infested with soybean aphid, 7 million of which were treated with insecticides (Ragsdale et al. 2007). Over 1.6 million acres (80% of total acreage) of soybean were treated for soybean aphid in Michigan in 2005 (Chris DiFonzo, personal communication). Broad-spectrum organophosphates and pyrethroids are typically used (DiFonzo and Hines 2002).

## Natural enemies of *A. glycines* in soybean

In its native range the soybean aphid is attacked by more than 30 species of predators, 8 species of aphidiine and aphelinid parasitoids, and several fungal pathogens (VandenBerg et al. 1997). In the U.S., the natural enemy complex is still developing; however, it is similar in structure with a large number of predatory species, several parasitoids and a few fungal pathogens.

### *Predators*

In U.S. soybean fields, predators supply the majority of the biocontrol (Fox et al. 2004, 2005, Costamagna and Landis 2007a, Costamagna and Landis 2007b, Costamagna et al. 2007a). Over 22 predatory taxa are known to attack soybean aphid in the north-central U.S. (Rutledge et al. 2004). This community is comprised of a large ground-dwelling community dominated by Carabidae species and a diverse community of foliage-foragers including species in the families: Cantharidae, Coccinellidae, Chamymaemyiidae, Syrphidae, Anthocoridae, Nabidae, Chrysopidae, and Hemerobiidae (Rutledge et al. 2004). Of these, the most numerous predators collected by Rutledge et al. (2004) were the minute pirate bug, *O. insidiosus* and the multicolored Asian lady beetle, *H. axyridis*. In Indiana, these species accounted for over 85% of the predators found in the field (Rutledge et al. 2004). The most common natural enemies found in Michigan soybean fields are: *O. insidiosus*, *H. axyridis*, *C. septempunctata*, and *H. convergens* (Fox et al. 2004, 2005, Costamagna and Landis 2007b, Costamagna et al. 2007a). In addition to these species, Kaiser et al. (2007) have found the cecidomyiid, *A. aphidomyza* and the syrphid species *Allograpta oblique* (Say), *Eupeodes americanus* (Wiedemann), *Syrphus rectus* (Osten Sacken), *Paragus haemorrhous* Meigen, *Eupeodes volucris* Osten Sacken, *Toxomerus marginatua* Say, and *Sphaerophorus contigua* attacking soybean aphid.

*Parasitoids*

In 2000-2002, parasitoids of *A. glycines* were nearly undetectable in north-central U.S. soybean production systems (Rutledge et al. 2004); however, in 2003, several parasitoid species were detected utilizing this new host. Kaiser et al. (2007) collected four parasitoid species from sentinel *A. glycines* on potted soybean plants placed in soybean fields at the Kellogg Biological Station, Hickory Corners, MI. These were (in order of abundance): *Lysiphlebus testaceipes* (Cresson), *Aphidius colemani* Viereck, *Aphelinus asychis* (Walker), and *A. albipodus* Hayat & Fatima. Despite the detection of parasitoids, they continue to play a small role in the conservation biological control of *A.*

*glycines*, accounting for less than 4% of the natural enemies found in 2003-2005 (Costamagna and Landis 2007a).

In 2007, releases of a non-native parasitoid *Binodoxes communis* initiated a classical biological control program for soybean aphid. Pre-release testing indicated a very low risk of non-target attack by this parasitoid (Wyckhuys and Heimpel 2007, Wyckhuys et al. 2007, Wyckhuys et al. 2008). Releases were made in Minnesota, Michigan and Iowa. Currently, it is unknown if released wasps have established.

### *Pathogens*

Entomopathic fungi may also play a role in suppressing aphid populations. Kaiser et al. (2007) commonly observed fungal pathogens attacking pea aphids in alfalfa and clover fields but the disease was rarely observed in soybean aphid found in adjacent fields. *Pandora neoaphidis* and *Conidiobolus thromboides* have also been isolated from *A. glycines*.

## Impact of natural enemies on *A. glycines* population dynamics

Understanding how the community of natural enemies present in the soybean agroecosystem affects *A. glycines* population dynamics is necessary for successful biological control. Predators can significantly reduce *A. glycines* adult establishment on soybean, and are more likely to cause reductions the later soybean aphid arrives in soybean fields (Costamagna and Landis 2007a, Costamagna et al. 2007a). The number of predators required to suppress *A. glycines* is low; in one experiment by Fox et al. (2004) total predator populations never exceeded 5 per $m^2$ yet prey populations were suppressed for half of the trial. This illustrates the potential importance of generalist predators in suppressing this pest when present at low densities (Fox et al. 2004). Costamagna and

Landis (2007a) compared the impact of top-down regulation of *A. glycines* by natural enemies with bottom-up impacts of agricultural management practices. Although no bottom-up impacts were detected, a strong top-down effect was found, indicating that generalist predators are important in the regulation of *A. glycines* (Costamagna and Landis 2007a).

Physiological and behavioral differences between natural enemies will affect their role in the biological control of *A. glycines*. Rutledge et al. (2004) contrasted two predators commonly found in soybean fields, *O. insidiosus* and *H. axyridis* that differ in their interactions with *A. glycines*. *Orius insidiosus* has a number of traits that suggest it primarily acts to suppress growing aphid populations (Rutledge et al. 2004). This generalist predator is present in soybean throughout the season where it increases in density until soybean plants senesce. *Orius insidiosus* can survive when aphid populations are low by feeding on soybean pollen and moisture and minerals from soybean phloem (Isenhour and Marston 1981, Armer et al. 1998). In contrast, *H. axyridis* can act to either prevent or to reduce high aphid densities as one of the first coccinellids to arrive in soybean fields in the spring (Ragsdale et al. 2004). *Harmonia axyridis* is capable of a distinct numerical response in the presence of abundant prey. Populations of this predator typically peak at or just after the population of aphid prey and exhibit a strong numerical response to soybean aphid, becoming more common in fields once aphids reach 100 or more per plant (Ragsdale et al. 2004).

## Within-field interactions and the soybean aphid food web

### *Intraguild predation (IGP)*

IGP is defined as predatory interactions between natural enemies occupying the same trophic level and competing for similar hosts/prey, which can shape the distribution, abundance, and evolution of intraguild competitors. IGP can lead to spatial and temporal exclusion of intraguild competitors, competitive coexistence or alternative stable states (Polis et al. 1997, Polis 1998). Biological theory has evolved considerably from simple models that state if beneficial insect species are sufficiently abundant herbivore populations will be suppressed, allowing plants to grow until limited by competition (Hairston et al. 1960). The assumption that the predator and parasitoid community regulating herbivores can be combined into a single trophic level, having a parallel effect on pest control is lacking in that it neglects complex, potential negative interactions, including IGP (Rosenheim et al. 1995, Rosenheim 1998, Colfer and Rosenheim 2001, Meyhofer 2001, Kindlmann and Houdkova 2006). In aphidophagous systems where several natural enemies compete for a single dominate extraguild prey, interactions such as IGP are likely to occur (Lucas 2005). Several studies have measured IGP of aphid parasitoids by aphid predators (Wheeler et al. 1968, Ferguson and Stiling 1996, Colfer and Rosenheim 2001, Meyhofer 2001, Snyder and Wise 2001, Snyder and Ives 2003, Snyder et al. 2004a, Kindlmann and Houdkova 2006). When the impacts of IGP on aphid biological control are evaluated across several systems, three potential outcomes are found: antagonistic (competition among natural enemies), additive (no competition, no facilitation), or synergistic interactions (facilitation) (Lucas 2005). These studies illustrate that IGP can have diverse effects on parasitoid populations and aphid suppression.

### *Predator-parasitoid interactions*

IGP of parasitoids by predators can disrupt biological control if an intraguild predator preferentially selects parasitized prey over unparasitized prey, or if the intraguild predator is inefficient at exploiting herbivores (Colfer and Rosenheim 2001). These conditions could cause the parasite population to be suppressed while herbivore populations expand (Ferguson and Stiling 1996, Colfer and Rosenheim 2001, Snyder and Ives 2003). Alternatively, if an intraguild predator is efficient at exploiting herbivore prey and selects unparasitized aphids over parasitized aphids or aphid mummies, herbivore regulation could be either unchanged or enhanced by IGP (Ferguson and Stiling 1996, Colfer and Rosenheim 2001, Snyder et al. 2004b, Kindlmann and Houdkova 2006). These differences illustrate the need for system-specific research to determine how IGP will affect biological control.

### *Predator-predator interactions*

Generalist predators can be effective biological control agents of native and exotic pests (Symondson et al. 2002); however, some interactions between predators can interfere with pest suppression (Snyder and Wise 1999). Snyder and Wise (1999) define interference among predators to include IGP, cannibalism, predator avoidance behavior, and predator-predator competition. Predators may function from the third trophic level, suppressing herbivores or from the fourth trophic level suppressing populations of intermediate predators through IGP and thereby potentially releasing herbivore populations from their top-down control (Rosenheim and Corbett 2003). Several factors may influence whether a predator is functioning at the third or fourth trophic level. These include encounter probabilities, attack probabilities, capture success, and consumption probabilities may affect prey choice of a predator, habitat structure and physical refuges, active prey defenses and predator preferences (Shi 1993).

Intraguild interactions between predators have been shown to cause diverse effects on prey population dynamics and plant productivity (Polis et al. 1989, Polis 1991, Rosenheim et al. 1995, Rosenheim 1998, Prasad and Snyder 2004, Snyder et al. 2004a). Venzon et al. (2002) studied the effects of *Orius laevigatus* (Fieber) on the population dynamics of the predatory mite *Phytoseiulus persimilis* Athias-Henriot and the spider mite *Tetranychus urticae* Koch on cucumbers. They found that although this predator killed large numbers of predatory mites and spider mites, the presence of *O. laevigatus* had little to no effect on mite abundance or cucumber plant fruit weight (Venzon et al. 2002). Snyder and Wise (2001) examined whether IGP weakens the ability of carabids and lycosids to control herbivores in gardens of cucumber and squash. In spring cucumber gardens, the presence of lycosids increased fruit production and decreased populations of cucumber beetle. Carabids weakly decreased cucumber beetle. In late season squash gardens, carabids increased fruit production by decreasing densities of squash bug. Lycosid spiders decreased squash yield by IGP of important hemiptern predators of the squash bug (Synder and Wise 2001). It appears that late season effects of carabids and spiders counteracted each other so that the complete guild did not influence squash fruit production. Snyder et al. (2004a) examined IGP between larvae of two exotic ladybeetles, *C. septempunctata* and *H. axyridis*, and two natives, *Coccinella transversoguttata* Brown and *H. convergens*. When the native ladybeetles were paired with either exotic species in microcosms they were more often the intraguild prey than predator. When the two exotics were placed together neither had a clear IGP advantage. Adding alternative prey did not alter the frequency and patterns of IGP among these coccinelids (Snyder et al. 2004a). This may be contributing to the speed with which these exotic lady beetles are displacing natives following invasion (Snyder et al. 2004a). Prasad and Snyder (2004) studied the effects of predator interference on the biological control of *Delia* sp. eggs by a community of ground-active beetles. They found that smaller staphylinid and carabids beetles commonly preyed upon fly eggs while larger beetles rarely ate eggs but did feed on the smaller beetles. Despite this IGP, the community of carabids and staphylinids decreased eggs survival (Prasad and Snyder 2004). A 4-fold increase in beetle community density did not lead to increased activity-density or egg predation (Prasad and Snyder 2004). Rosenheim et al. (1993) found that generalist hemiptern predators decreased the survival of lacewing larvae. Experimental addition of the reduviid *Zelus renardii* (Kolenati) or *Nabis* sp. (*Nabis alternatus* Parshley and *N. americorfurus* Carayon) generated sufficient lacewing larval mortality to release aphid (*Aphis gossypii*) populations from their control (Rosenheim et al. 1993).

### A conceptual framework of IGP and foraging behavior

Rosenheim and Corbett (2003) identify encounter frequency as a key factor contributing to the diet of extreme generalists that attempt to capture and consume any available prey they encounter. Encounter frequencies are highly influenced by foraging behavior. When two predatory strategies are examined, sit-and-wait predation versus active foraging, they suggest that foraging strategy will influence the type of prey selected by a predator. Sedentary prey are consumed by widely foraging "intermediate" predators which may in turn be captured by sit-and-wait "top" predators. Mobile prey may be consumed by either foraging or sit and wait predators.

Rosenheim and Corbett (2003) tested these ideas by developing a mathematical model based on a papaya community consisting of a sedentary herbivore, *Tetranychus cinnabarinus* (Boisduval), which feeds on papaya foliage, two intermediate predators, *Stethorus siphonulus* (Kapur) and *Phytoseiulus macropilis* (Banks), both widely foraging specialists of spider mites, and the sit and wait omnivorous predator *Nesticodes rufipes* (Lucas), a tangle-web spider. They found that foraging predators have the potential to be effective regulators of herbivore populations, even when they also act as omnivores consuming other predators. Sit-and-wait predators are unlikely to suppress populations of sedentary herbivores by foraging heavily on intermediate predators. Sit-and-wait predators are predicted to function as the top predators, suppressing populations of intermediate predators and releasing sedentary herbivore populations from their control (Rosenheim and Corbett 2003).

These above model predictions were confirmed through field experiments (Rosenheim et al. 2004). The widely foraging *P. macropilis* was capable of generating strong suppression of *T. cinnabarinus* populations. Second, the sit-and-wait predator *N. rufipes* never produced detectable levels of spider mite suppression. *Nesticodes rufipes* consumed both of the foraging predators. Spider mite suppression by *S. siphonulus* was vulnerable to disruptive effects of *N. rufipes* whereas suppression by *P. marcropilis* was relatively insensitive to *N. rufipes*. This difference was attributed to the difference in body size between these two intermediate predators. *Phytoseiulus macropilis* is smaller and thus consumes less prey and forages less leading to less frequent encounters with *N. rufipes* webs compared with *S. siphonulus* (Rosenheim et al. 2004).

### IGP in the *A. glycines* system

The model proposed by Rosenheim and Corbett (2003) can be modified to incorporate intraguild interactions within the community of generalist predators in soybean. As with the model system, soybean is fed upon by a sedentary herbivore, the soybean aphid which in turn is prey for several intermediate predators. In soybean, however, two groups are discernable among these. Resident intermediate predators are arthropods which are predatory as larvae, spending their juvenile stage feeding primarily on the soybean aphid. Important predators in this group include the larvae of ladybeetles, lacewings, syrphids, aphid predatory midge, and *Orius* nymphs. A second group of intermediate predators, the transients, search for prey in several crops within a growing season, foraging for prey in soybean for shorter durations. These species move into soybean when soybean aphid is present, feed for some time, then move on, leaving some resident population of aphids behind. Important species in this group include adult *C. septempunctata and H. axyridis.*

A critical time period in the biological control of soybean aphid occurs in the early season when aphid populations begin to colonize soybean plants. When aphid populations are low, adult *H. axyridis* and *C. septempunctata* move through soybean fields feeding within patches of soybean aphid, but are not stimulated to lay eggs. They will spend short feeding bouts within an aphid patch, removing some of the population before moving on to other soybean fields or to search for prey in other crops. During this period, when ladybeetles are highly mobile IGP events occurring between these transient predators and resident predacious larvae could influence the success of soybean aphid biological control.

### Impacts of landscape variables on insects in agroecosystems

Agricultural landscapes have changed dramatically with agricultural intensification, resulting in larger more contiguous fields and non-crop areas reduced in area and frequency (Bianchi et al. 2006). The diversity and abundance of natural enemies and the biocontrol services they provide are influenced by the structure and composition of the surrounding landscape (Marino and Landis 1996, Colunga-Garcia et al. 1997, Bommarco 1998, Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharntke 2005, Tscharntke et al. 2005b). Landscape variables such as habitat complexity, habitat quality, and patchiness as well as an organism's dispersal capability all influnce the ability of a landscape to support biological control in agricultural croplands (Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharntke 2005). Moreover, agricultural crop fields are ephemeral habitats in which anthropogenic disturbances such as tillage, pesticide application, and harvesting require arthropods to frequently re-colonize crops (Wissinger 1997). The surrounding landscape provides the local species pool of arthropods for this re-colonization and thus may influence the level of biological control in frequently disturbed crop fields (Lee et al. 2001).

In a recent review, Bianchi et al. (2006) found that increased landscape complexity reduced pest pressure in 45% of the studies. Effects included reductions in pest density (Ostman et al. 2001, den Belder et al. 2002) and reduction in crop injury (Thies and Tscharntke 1999, Thies et al. 2003). Pest pressure increased with landscape complexity in 15% of the cases examined (Raffy and Tran 2005, Roschewitz et al. 2005), but the two were unrelated in 40% of the studies (Galecka 1966, Holland and Fahrig 2000, Klug 2003, Thies et al. 2005). It is likely that some of this variation is tied to differences in the impact of landscape complexity on specific natural enemy populations. A more detailed understanding of how natural enemies respond to landscape structure may help us understand these outcomes. The majority of the work thus far has focused on response to overall landscape complexity (percent non-crop habitat), habitat thresholds, edge effects, and habitat dispersal via landscape corridors.

*Habitat complexity*

The diversity of crop and non-crop habitats within a landscape can greatly affect communities of herbivores and their natural enemies within an agricultural crop (Fahrig 1992, Marino and Landis 1996, Colunga-Garcia et al. 1997, Bommarco 1998, Elliott et al. 1999, Menalled et al. 1999, Thies and Tscharntke 1999, Fahrig 2001, den Belder et al. 2002, Ostman 2002, Tscharntke et al. 2002, Fahrig 2003, Menalled et al. 2003, Thies et al. 2003, Weibull et al. 2003, Schmidt et al. 2004, Tscharntke and Brandl 2004, Schmidt et al. 2005a, Schmidt et al. 2005b, Tscharntke et al. 2005b, Tscharntke et al. 2005a). For example, Colunga-Garcia et al. (1997) studied changes in species assemblages of predatory coccinellids in response to landscape structure with different mosaics of cultivated (alfalfa, corn, wheat) and uncultivated (deciduous forest, field succession) habitats. Species composition differed between sites with and without deciduous forest habitat (Colunga-Garcia et al. 1997). Although the deciduous forest habitat had the highest ladybeetle species richness (*Cycloneda munda* (Say), *Chilocorus stigma* (Say), and *Brachiacantha ursine* (F.) most abundant in deciduous habitat), there were exceptions. *Coccinella septempunctata* was the dominant species in the landscape and was equally abundant all sites, whereas *Coleomegilla maculate* lengi Timberlake was more abundant in the site with corn habitat (Colunga-Garcia et al. 1997). Fahrig and Jonsen (1998) found that in a study of 31 alfalfa fields in an agricultural landscape, more isolated fields had overall higher insect species richness. Similarly, Elliott et al. (1998) used aerial photographs to demonstrate that increases in uncultivated land and in patchiness surrounding wheat fields were both associated with increasing abundance and richness in predator communities in wheat fields. Bommarco (1998) found that the fecundity of the generalist predatory carabid, *Pterostichus cuperus*, was greater in areas with small fields, higher perimeter-to-area ratios, and a higher coverage of perennial crops compared to less spatially complex areas.

### *Minimal suitable habitat thresholds*

Several studies suggest thresholds in landscape structure may exist below which the search efficiency and the ability of natural enemies to aggregate and control pests is diminished (With and King 1999). Simulation experiments have shown that search success of natural enemies declined when suitable habitat fell below 20% (With and King 1999). Tenebrionid beetles (*Eleodes obsolete*) and small crickets (*Acheta domestica* L.) also exhibited threshold responses in movement when habitat fell below 20% (Wiens et al. 1997, With et al. 1999). Parasitism rates also decline in agricultural landscapes when the non-crop area falls below 20% (Thies and Tscharntke 1999).

### *Edge effects*

Habitat edges that border agricultural fields could influence natural enemy diversity and abundance by providing alternative food resources, shelter, and/or protection. Natural enemy populations can build up in field borders and move into the crop when pest populations begin to build. However, habitat edges may also impede the movement of arthropods into crops by acting as a physical barrier by providing a more stable and suitable habitat than the crop (Fortin and Mauffette 2001). A substantial amount of research has been done to understand the role of field edges on the biological control of pests by natural enemies (Alomar et al. 2002). Overall, these data show that measuring the activity and richness of predatory populations in field boundaries can, but doesn't always accurately predict their potential impact on herbivores in neighboring crops.

*Corridors and habitat connectivity*

A popular strategy for maintaining populations of plants and animals in fragmented landscapes is to connect isolated patches with thin strips of habitat called corridors. Corridors are thought to increase gene flow, promote reestablishment of locally extinct populations, and increase species diversity within otherwise isolated areas (Tewksbury et al. 2002). Collinge and Palmer (2002) tested the theory that isolated habitat patches will experience greater rates of species loss compared with less isolated habitats. Corridors did not significantly influence overall rates of patch colonization, but slightly increased the probability of colonization by less vagile species (Collinge 2000). Collinge (2000) also characterized individual movement pathways of three insect species in plots with and without corridors. One of the three species significantly preferred corridors, whereas the other two species moved independently of corridors. These results suggest that corridors have the potential to promote movement of organisms among habitat patches, but that their function may depend upon species characteristics, landscape context, patch size, and environmental variation.

## Functional spatial scale and trophic level

Landscape complexity may not influence all species equally, or at the same scale (den Belder et al. 2002, Steffan-Dewenter et al. 2002, Thies et al. 2003, Schmidt et al. 2005a). Thies et al. (2003) and others have hypothesized that interacting communities are made up of species with different spatial strategies. The spatial scale experienced by an organism may depend on its trophic level (Holt et al. 1999). Holt et al. (1999) suggest that plant species occupy distinct microhabitats whereas herbivores have larger spatial domains, but are confined to local communities. Predators and parasitoids can utilize ranges that encompass the habitats of several prey species (Holt et al. 1999). There is no absolute size for a landscape from an organism-centered perspective; the size of a landscape varies depending on what constitutes a mosaic of habitat or resource patches meaningful to that particular organism. Thies et al. (2003) measured the functional spatial scale at which the rape pollen beetle, *Meligethes aeneus* F. and its parasitoids are affected by their landscape. They tested the effects of landscape on trophic-level interactions using simple (<3% non-crop habitat) to complex (>50% non-crop habitat) landscapes, analyzed them at 8 spatial scales (concentric circles 0.5-6 km in diameter), and found that herbivory and parasitism were correlated with percent non-crop area using a spatial scale of 1.5 km. At all spatial scales, the predictive power of non-crop area was higher for herbivory than for parasitism. Schmidt et al. (2005) used pitfall traps to collect spider species in wheat fields located in landscapes that varied in their proportion of non-crop habitat. Although the proportion of non-crop habitat did not affect the abundance of spiders, a relationship was detected between non-crop habitat and species diversity. Spider species richness in wheat fields rose with the proportion of non-crop habitat in the surrounding landscape (Schmidt et al. 2005). The most common family of spiders collected was the Lycosidae. Ballooning species (majority of Linyphiidae, Araneidae, and Theridiidae), with the exception of *Erigone atra* and *Erigone dentipalpis* were poorly represented, suggesting that ballooning species may respond to a larger spatial scale of landscape complexity compared with walking species (Schmidt et al. 2005).

### Influence of landscape variables depends on farming practice

A potential complication of studying the effects of landscape complexity in agricultural systems is the effects production practices can have on arthropod communities. Weibull et al. (2003) compared the effect of farm management (conventional farming versus organic) and landscape features on species richness in cereal fields, leys (arable field temporary with perennial grass and clover mowed 2-4 times a year), and semi-natural pastures. The effects of landscape were more pronounced on conventional farms, species richness of plants, butterflies, and carabids increased with small-scale landscape heterogeneity or the amount of field margin (perimeter to area ratio). There were no significant correlations between species richness and landscape variables among organic farms. The impact of predators (carabids, rove beetles, and spiders) on the bird-cherry oat aphid *Rhopalosiphum padi* (L.) depended on a high perimeter-to-area ratio and high percentage of perennial crops in effective early season control of the aphid (Weibull et al. 2003).

Ostman et. al (2001) also measured the impact of natural enemies on the population development on the bird cherry-oat aphid on conventional and organic farms. They found that natural enemies had a greater impact on *R. padi* establishment on organic farms than on conventional farms. Irrespective of farming system, landscapes with abundant field margins and perennial corps were associated with low *R. padi* establishment. After establishment, there was no difference in ground-living enemy impact on *R. padi* population growth rate between farming systems, but impact was greater in landscapes where arable land was contiguous (Ostman et al. 2001).

## Impacts of the agricultural landscape in the soybean system

The landscape of the north-central U.S. soybean growing region is a mosaic of crop and non-crop habitats, containing both primary and secondary hosts of *A. glycines*. Habitat complexity of a landscape, the spatial arrangement of crop and non-crop habitats, edge effects, and habitat connectivity within a landscape can greatly influence soybean aphid movement between its winter and summer host plants. Soybean fields are ephemeral habitats where disturbances such as tillage, pesticide application and harvesting force repeated re-colonization by soybean aphid and its natural enemies. The surrounding landscape acts as a source of both. To aid in the development of a successful biological control program for *A. glycines,* this study investigated how the proportion of an agricultural landscape comprised of non-crop habitat influenced aphid abundance within soybean fields.

## Summary

The soybean aphid is an invasive pest that was first detected in the U.S. in 2000. This pest is attacked by a large guild of native and exotic predators throughout its invaded range. Successful control of soybean aphid requires early season suppression by predators. To improve management of soybean aphid we must understand the influence of landscape composition in supplying predators to crop fields. In addition, interactions between species within the soybean aphid food web must be investigated to determine how these influence the net biocontrol service provided. This dissertation aims to highlight the importance of understanding species-specific relationships with the landscape and illustrate the importance of conserving natural habitats in promoting successful pest management in agricultural systems.

# CHAPTER 2

# IMPACT OF INTRAGUILD PREDATION BY ADULT *HARMONIA AXYRIDIS* (COLEOPTERA: COCCINELLIDAE) ON *APHIS GLYCINES* (HEMIPTERA: APHIDIDAE) BIOLOGICAL CONTROL IN CAGE STUDIES.

## Abstract

The soybean aphid, *Aphis glycines* Matsumura, has become a principal arthropod pest of soybean in the U. S. since its first detection in 2000. This species threatens soybean production through direct feeding damage and virus transmission. A diverse guild of insect predators feeds on soybean aphid in Michigan including the exotic coccinellid *Harmonia axyridis*, the native gall midge *Aphidoletes aphidimyza* and the native lacewing *Chrysoperla carnea*. In addition to feeding on *A. glycines* some members of this guild may also engage in intraguild predation. These interactions may produce positive, negative, or neutral impacts on *A. glycines* biological control. I explored the impact of intraguild predation on soybean aphid population dynamics by comparing aphid populations in microcosms with either *A. aphidimyza* larvae or *C. carnea* larvae alone, with both a *H. axyridis* adult and either *A. aphidimyza* or *C. carnea* larvae, and without predators. When *H. axyridis* was present with larval *A. aphidimyza* or *C. carnea*, the lady beetle acted as an intraguild predator. However, intraguild feeding did not result in a release of aphid populations compared with microcosms containing only the intraguild and aphid prey. A similar result was found in field cages. Cages allowing large predators had reduced numbers of *A. aphidimyza* and *C. carnea* larvae but also significantly fewer aphids compared with predator exclusion cages. Thus, in both lab

and field studies the direct impact of *H. axyridis* on *A. glycines* overcame its negative impact as an intraguild predator. Together, these studies indicate that although the exotic *H. axyridis* does act as an intraguild predator and may contribute to local declines in *A. aphidimyza* and *C. carnea*, it is also currently important in overall biological control of *A. glycines*.

## Introduction

In agricultural systems, knowledge of food web interactions is often limited due to the complexity of tri-trophic relationships and the number of species involved (Bascompte and Melian 2005). Invasions of exotic species are likely to profoundly affect the structure of food webs in agroecosystems. The soybean aphid, *Aphis glycines* Matsumura, a native of Asia, was first detected in the U. S. in Wisconsin in July of 2000. Its range now extends throughout the north-central soybean growing states and into Canada. Feeding by *A. glycines* on the leaves, stems, and pods of the soybean plant causes reductions in photosynthetic rate, plant growth, and seed yield of soybean plants (DiFonzo and Hines 2002). This pest can also vector several viruses, including alfalfa mosaic, soybean dwarf, soybean stunt, soybean mosaic, tobacco ringspot, and bean yellow mosaic (VandenBerg et al. 1997, Clark and Perry 2002, Wang and Ghabrial 2002).

In this system, the invading community extends beyond soybean aphid, involving the introduction, both intentional and unintentional, of an entire exotic food web (Thompson and Townsend 2003). The primary host plants of soybean aphid are buckthorn species in the genus *Rhamnus,* the most abundant and widespread species is *R. cathartica* L. (Rhamnaceae), a native to Asia introduced in the 1880's as a landscape plant (Yoo et al. 2005). The secondary host plant of *A. glycines*, cultivated soybean, *Glycine max* L. (Fabaceae) (also native to Asia), has been cultivated in the US since the early 1800's, and is one of the dominant crops in the north-central region. The guild of predators that attack soybean aphid also contains non-native species, including the following coccinellids: *Harmonia axyridis* Pallas, *Coccinella septempunctata* L. and *Hippodamia variegata* (Goeze) (Gardiner and Parsons 2005). These organisms interact with native predatory species including the coccinellids, *Coleomegilla maculata* (DeGeer), *Hippodamia convergens* Guérin-Méneville, *Hippodamia parenthesis* (Say), the lacewing *Chrysoperla carnea* (Stephens) and *Aphidoletes aphidimyza* (Rondani) (Cecidomyiidae) that have adapted to utilizing soybean aphid as prey.

### *Intraguild interactions*

In aphidophagous systems where several predators compete for a single dominant prey, interactions such as intraguild predation are likely to occur (Lucas 2005). Intraguild predation (IGP hereafter), is defined by Lucas et al (1998) as predatory interactions between predators within a guild. Generalist predators can be effective biological control agents of native and exotic pests (Symondson et al. 2002); however, interactions such as IGP can also interfere with pest suppression (Snyder and Wise 1999). Intraguild interactions between predators have resulted in diverse effects on prey population dynamics and plant productivity (Polis et al. 1989, Polis 1991, Rosenheim 1998, Prasad and Snyder 2004, Snyder and Clevenger 2004, Snyder et al. 2004a). Overall, these studies indicate that the impacts of IGP are community specific. As one of the most abundant predators found in soybean fields (Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2007a), *H. axyridis* has the potential to impact both *A.*

*glycines* population dynamics and populations of native predators that have adapted to utilizing soybean aphid as a food source.

There is abundant evidence that *H. axyridis* acts as an intraguild predator of other coccinellids and populations of some native species have declined significantly after the establishment of exotics (Elliott et al. 1996, Colunga-Garcia and Gage 1998, Michaud 2002). Although IGP by *H. axyridis* on other predator groups has received less attention; this study focuses on the intraguild interactions between *H. axyridis*, *C. carnea*, and *A. aphidimyza*. Previous studies have found that IGP by lady beetles on lacewing and *A. aphidimyza* larvae did occur in microcosm studies but not under field conditions. Lucas et al. (1998) established that the lady beetle *C. maculata* was an intraguild predator of both *Chrysoperla rufilabris* (Burmeister) and *A. aphidimyza* in microcosms. In the field, Brown (2003) compared aphid predator composition before and after the introduction of *H. axyridis* in apple orchards and found no effect of *H. axyridis* on *A. aphidimyza* and chrysopid populations.

*Impact of IGP on early season biological control*

A critical time in the biological control of soybean aphid occurs in the early season when aphids begin to colonize soybean plants. We have observed that when aphid populations are low and patchy, adult *H. axyridis* act as "transient predators," spending short feeding bouts within an aphid colony, removing some of the aphid population before moving on to feed elsewhere (Landis unpublished data). Through a review of mark-recapture studies this behavior was also described by Evans (2003) who stated that coccinellids often do not remain long in any one location and will forage in many different habitats throughout their breeding season. When aphid populations are low, adult coccinellids are less likely to lay eggs (Evans 2003); therefore lady beetle larvae are not yet abundantly present in soybean fields. My hypothesis was that during this early season time period *H. axyridis* adults may release soybean aphid populations from overall control by acting as intraguild predators of smaller "resident predators", including larvae of the aphid predatory midge *A. aphidimyza* and green lacewing *C. carnea*. As immature stages these species have limited mobility; individuals in soybean fields spend their entire juvenile stage feeding primarily on the soybean aphid on a single plant or foraging among a few plants within a field. If *H. axyridis* acts as an intraguild predator and removes the majority of these small resident predaceous larvae, the remaining aphids could be released from overall control. However, if *H. axyridis* feeds primarily on aphids, these species may have an additive negative effect on *A. glycines* populations. The objectives of this study were to: 1) investigate how the presence of *H. axyridis* impacts populations of the native predators *A. aphidimyza* and *C. carnea* in soybean agroecosystems and 2) determine if IGP among these arthropods impacts soybean aphid population dynamics.

## Methods

### *Rearing*

Soybean plants var. 92B16 (Pioneer Hi-Bred International Inc., Johnston, IA) were maintained in a greenhouse at 24°C on a 16:8 h L:D. Soybean aphid was cultured on soybean in a walk-in growth chamber (Percival Scientific, Perry, IA) at 24°C:16°C on a 16:8 h L:D. The predatory midge, *A. aphidimyza*, was obtained from IPM Laboratories (Locke, NY) as pupae. Flies were hatched by placing the pupae into a dark growth chamber for 48 h at 24°C. Adults were released onto soybean aphid-infested soybean plants and allowed to lay eggs. Larvae hatched within 3 d and reached their second instar within 5 d. The aphid predator *C. carnea* was obtained from Koppert Biological Systems (Ann Arbor, MI) as eggs and first instar larvae. The eggs and larvae were placed in rearing boxes on soybean plants infested with *A. glycines*. A culture of *H. axyridis* was initiated by field-collecting adult beetles from soybean fields at the Michigan State University Beet and Bean Farm (Saginaw, MI); larvae and adult *H. axyridis* were reared separately on soybean aphid-infested plants. All predator colonies were maintained at 24°C:16°C on a 16:8 h L:D.

*Predator consumption rates*

Aphid consumption rates of *A. aphidimyza* and *C. carnea* were measured in 60 x 15 mm Petri dish arenas. The bottom of the dish was lined with moist filter paper and contained a soybean leaflet infested with 30 second instar or adult *A. glycines*. One second instar *A. aphidimyza* or second instar *C. carnea* was added to each arena and allowed to forage for 24 h, after which the predator was removed and the number of remaining aphids recorded. Five replications of each treatment were arranged randomly on a cafeteria tray and held in a walk-in growth chamber at 24°C:16°C on a 16:8 h L:D.

*Microcosm design*

Microcosms consisted of a 3.79 L cylindrical-shaped clear plastic container with three 7 x 13 cm windows of fine mesh netting. The container had a 10 cm opening. The plastic container was inverted over a 10 cm square plastic pot containing three V1 soybean plants (Teare and Hodges 1994). The opening of the container was held inside the pot; it was buried in the soil and sealed with tape. Microcosms were held on cafeteria trays in a walk-in growth chamber at 24°C:16°C on a 16:8 h L:D and watered by filling the tray with water.

*Microcosm experimental procedure*

The microcosm experiments were designed to measure the intensity of IGP by the transient predator *H. axyridis* on the resident predators *A. aphidimyza* and *C. carnea* and the resulting impact on *A. glycines* population dynamics. The interaction between *H. axyridis* and the two resident larval predators was evaluated in separate experiments. In both the *A. aphidimyza* and *C. carnea* microcosm experiments four treatments were compared. For *A. aphidimyza* the treatments were: aphids alone (CONTROL), aphids + *A. aphidimyza* (AA), aphids + *H. axyridis* (HA), and aphids + both predators (*H. axyridis* and *A. aphidimyza*) (BOTH). The treatments for the *C. carnea* experiment were: aphids alone (CONTROL), aphids + *C. carnea* (CC), aphids + *H. axyridis* (HA), and aphids + *H. axyridis* and *C. carnea* (BOTH).

To begin a microcosm experiment, 10 adult and 5 second instar aphids were placed onto clean leaf disks. One disk was then attached to a fully expanded leaf on each of three plants within a pot, for a total of 45 aphids per microcosm. After 48 h, aphids were counted in each microcosm, and in the *A. aphidimyza* experiment one second instar *A. aphidimyza* was introduced onto each of the three soybean plants per microcosm in the AA and BOTH treatments. Similarly, in the *C. carnea* experiment one second instar *C. carnea* was introduced onto each of the three soybean plants per microcosm in the CC and BOTH treatments 48 h after the introduction of *A. glycines*. This was considered the beginning of the experiment, time 0 in all analyses. In the *A. aphidimyza* experiment aphids averaged (± 1 SEM) 114.47 ± 6.97 (CONTROL), 113.33 ± 6.85 (AA), 116.2 ±

7.11 (HA), and 107.8 ± 6.51(BOTH) at time 0 h. In the *C. carnea* experiment *A. glycines* averaged 123.27 ± 10.41 (CONTROL), 111.47 ± 8.24 (CC), 129.4 ± 7.14 (HA), and 119.8 ± 8.57 (BOTH) at 0 h. In both experiments, 24 h after the release of the larval predators aphids were counted again in all treatments and one adult *H. axyridis* was released into the HA and BOTH microcosm treatments. The beetle was allowed to forage for 3 h, after which it was removed to simulate its transient feeding behavior in the field. During this 3 h *H. axyridis* had the opportunity to consume *A. glycines* (HA treatment), or both aphids and the larval predators (BOTH treatment). After the removal of *H. axyridis*, aphids were counted in the HA treatment and aphids and *A. aphidimyza* or *C. carnea* were counted in the BOTH treatment. Aphids were then counted daily in all treatments for the following two d and again every 48 h for an additional two sampling periods to track aphid population growth in each treatment.

### *Field cage experiment*

To determine how the intraguild interactions examined in the microcosm experiment compared with interactions in the field, where a larger complex of generalist predators was present, a field cage experiment was conducted. In the field, *H. axyridis* was one of the two large exotic lady beetle predators, with *C. septempunctata* also abundant. These two coccinellids are both potential intraguild predators of a large community of small resident predators, including syrphid fly larvae, coccinellid larvae, and *O. insidiosus* adults and larvae in addition to *A. aphidimyza* and *C. carnea* larvae. Three treatments were designed to measure how IGP by large lady beetle adults on small predators impacted *A. glycines* populations. The three treatments were: a predator exclusion cage, preventing all predators from accessing aphid populations, a medium-mesh cage that allowed small predators to gain access to the cage but excluded large lady beetle adults, and a large-mesh cage that allowed access by both large lady beetles and small predators.

### *Cage design*

All cages consisted of 1 $m^3$ PVC frames with mesh enclosures that varied in the size of the mesh on the sides of the cage. The predator exclusion cage was made entirely of no-see-um netting (Venture Textiles, Braintree, MA). The medium- and large-mesh cages had no-see-um netting roofs and cage sides made from either 2 mm mesh (medium-mesh treatment) or 6 mm mesh (large-mesh treatment) (U.S. Netting, Erie, PA). All cages were lined at their base with Velcro attached to a plastic barrier buried to secure the cages at the soil surface and prevent entry of ground-dwelling predators. The cages were arranged in a completely randomized design with three replicates of each treatment in a soybean field planted in 38.1 cm rows with soybean variety 92B16 (Pioneer Hi-Bred International Inc., Johnston, IA) at the Entomology Research Farm at Michigan State University (East Lansing, MI). Each cage contained two rows of plants, with an average of 25.3 plants per cage. When the cages were established aphid density averaged 22.2 per plant. All predators were hand-removed from caged plants prior to beginning the experiment.

### *Sampling procedure*

All cages were sampled weekly for 4 wks. A sample consisted of five plants that were randomly selected in each cage. Each plant was examined and the number of apterous and alate aphids and diversity and abundance of predators was recorded.

### *Statistics*

In the microcosm experiments, we compared the change in the number of *A. aphidimyza* and *C. carnea* before and after exposure to *H. axyridis* using a 2-sample t-test. A repeated-measures mixed model analyses of variance (ANOVA) was used to compare differences in aphid abundance between microcosm treatments. Block was included as a random effects factor and treatment, time, and their interaction as fixed effects factors. Differences in aphid and predator abundance between treatments were assessed by comparing least squares means. Aphid counts were square-root transformed prior to analysis to meet the assumptions of the model.

In the field cage experiment, the impact of excluding either large coccinellid predators (*H. axyridis* and *C. septempunctata*) or all predators on aphid populations was assessed using a repeated measures ANOVA random coefficients model with time included as a covariate and random effects for subject and subject-specific slopes on time. Based on residual analysis aphid data were square-root transformed to meet the assumptions of the model. Variation in the abundance of predators was also assessed using a repeated measures ANOVA random coefficients model with time included as a covariate and random effects for subject and subject-specific slopes on time. A square-root transformation was applied to predator means prior to analysis to meet the assumptions the model. Differences in aphid and predator abundance between treatments were assessed by comparing least squares means. Both the microcosm and field cage analyses were conducted using the PROC MIXED procedure of SAS version 9.1 (SAS Institute Inc. 1999).

## Results

*Predator consumption rates*

Second instar *A. aphidimyza* consumed on average 6.2 h± 1.71 second instar and 9.4 ± 0.4 adult *A. glycines* per 24 h, while second instar *C. carnea* consumed 17 ± 4.06 second instar and 3.4 ± 0.98 adult aphids per 24 h.

*Aphidoletes aphidimyza and H. axyridis*

In the *A. aphidimyza* and *H. axyridis* microcosm experiment, aphid populations in the CONTROL and HA treatments, both of which initially contained no predators, rose in the first 24 h while AA and BOTH treatments which contained *A. aphidimyza* remained relatively constant during this time period (Figure 2.1). At 27 h, i.e. after introduction and 3 h of feeding by *H. axyridis*, aphid populations in both the HA and BOTH treatments declined. During its 3 h presence, *H. axyridis* acted as an intraguild predator, significantly reducing numbers of *A. aphidimyza* larvae (t=6.87, df=14, $P<0.0001$) in the BOTH treatment. At time 24 h an average of 2.87 ± 0.09 midges were found in the AA and BOTH treatments. An average of 1.80 ± 0.26 midge larvae per microcosm were removed by *H. axyridis* during 3 h of foraging, leaving only 1.06 ± 0.23 midges per microcosm at 27 h in the BOTH treatment.

From 27-168 h overall aphid populations increased but were not consistent in all treatments as indicated by a significant interaction between treatment and time ($F_{16,308}$ = 3.00, P=0.0001). In the AA treatment, *A. aphidimyza* reduced aphid populations relative to the control beginning at 48 h and continuing until the end of the experiment (Figure 2.1). In this treatment *A. aphidimyza* reduced aphid populations in the first 48 h of the experiment (107.8 ± 6.51 aphids per microcosm at 0 h to 87.93 ± 7.84 aphids per microcosm at 48 h) but after 48 h aphid populations increased, reaching 372.33 ± 30.0 aphids per microcosm by 168 h. Three h of *H. axyridis* feeding in the HA treatment also significantly reduced aphid abundance, from 140.53 ± 9.31 aphids per microcosm at 24 h to 91.47 ± 7.97 per microcosm at 27 h. Following the removal of *H. axyridis*, aphid populations in the HA treatment increased and were not significantly different from the AA treatment from 48 h to 120 h. At 168 h the HA treatment had significantly higher aphid populations compared with the AA and BOTH treatments. In the BOTH treatment aphid population remained constant over the first 24 h in the presence of *A. aphidimyza*. Three hours of feeding by *H. axyridis* reduced *A. glycines* populations in the BOTH treatment from 107.47 ± 6.06 to 75.86 ± 7.6. The BOTH treatment was similar to the AA treatment throughout the experiment and significantly lower than the HA treatment beginning at 48 h and continuing through 168 h (Figure 2.1).

*Chrysoperla carnea and H. axyridis*

In the *C. carnea* and *H. axyridis* microcosm experiment, aphid populations increased in the CONTROL and HA treatments and remained relatively constant in the CC and BOTH treatments (Figure 2.2). As in the *A. aphidimyza* microcosm experiment, there was a significant treatment by experimental time interaction ($F_{16,308} = 16.67$, $P<0.0001$). Initially, aphid populations increased in all treatments, both in the CONTROL and HA treatments which did not contain any predators at the beginning of the experiment and in the CC and BOTH treatments which contained *C. carnea* larvae. At time 24 h *H. axyridis* was added to the HA and BOTH treatments, resulting in a decline in aphid numbers in these treatments by time 27 h. During its 3 h presence, *H. axyridis* acted as an intraguild predator significantly reducing numbers of *C. carnea* larvae (t=2.82 df=14, *P*=0.014) in the BOTH treatment. At time 24 h an average of 2.26 ± 0.12 and 2.6 ± 0.13 lacewings per microcosm were found in the RP and BOTH treatments respectively. The intraguild predator *H. axyridis* removed an average of 1.07 ± 0.28 lacewing larvae within 3 h of foraging, leaving 1.67 ± 0.29 lacewing larvae per microcosm in the BOTH treatment at 27 h. In the CC and BOTH treatments aphid populations were significantly lower than the CONTROL beginning at 48 h and continuing throughout the experiment (Figure 2.2). In the CC treatment aphid populations decreased between 48 h and 120 h and then began to increase ending the experiment at 179.13 ± 64.90 aphids per microcosm at 168 h (Figure 2.2). Despite the IGP, aphid populations in the BOTH treatment were relatively constant from 48 h to 120 h (139.0 ± 18.89 aphids per microcosm at 48 h to 141.33 ± 34.13 aphids per microcosm at 120 h) at which time populations began to increase reaching 168.53 ± 61.96 aphids per microcosm at 168 h.

*Field cage experiment*

Aphid populations increased in all three field cage treatments (Figure 2.3), however the impact of these treatments on aphid populations was not consistent across the 4 weeks of the experiment, as indicated by a significant treatment-by-time interaction ($F_{6,9}$=3.79, *P*=0.036). By wk four, aphid populations were significantly lower in the large-mesh treatment compared with the predator exclusion treatment (Figure 2.3). Allowing access to *C. septempunctata* and *H. axyridis* delayed aphid populations from reaching the economic threshold of 250 aphids per plant by two wks in the large-mesh treatment compared with populations in the medium-mesh and predator exclusion treatments. Adult *H. axyridis* and *C. septempunctata* were found only in the large-mesh treatment, indicating that they were effectively excluded from the medium-mesh and predator exclusion treatments. Populations of large lady beetles were low throughout the experiment, peaking at 0.4 ± 0.24 per plant on July 21. The population composition of large coccinellids in the large-mesh treatment was 55% *C. septempunctata* and 44% *H. axyridis*. Coccinellid larvae were found in both the medium- and large-mesh treatments and the difference in their abundance between the two treatments varied across time, indicated by a marginally significant interaction ($F_{3,12}$=3.33, P=0.056). Coccinellid larvae were significantly more abundant in the large-mesh treatment on July 21 reaching 1.47 ± 0.48 per plant compared with 0.07 ± 0.07 per plant in the medium-mesh treatment. Their populations were similar in the two treatments on the other three sampling dates (Figure 2.4). *Harmonia axyridis* was the most abundant species of coccinellid larvae found, averaging 0.05 ± 0.28 per plant in the medium-mesh treatment and 0.32 ± 0.09 per plant in the large-mesh treatment. Larvae of *C. septempunctata* were the second most abundant species, averaging 0.02 ± 0.02 per plant in the medium-mesh treatment and 0.06 ± 0.05 per plant in the large-mesh treatment. Lacewing larvae were only detected in the medium-mesh treatment, at 0.4 ± 0.16 larvae per plant on July 21. There was no difference in the number of *A. aphidimyza* found in the medium- and large-mesh treatments on any dates ($F_{1,4.5}$=0.19, P=0.679) (Figure 2.5). We were unable to restrict *O. insidiosus* from entering the predator exclusion treatment. There was a significant interaction in the abundance of *O. insidiosus* between the three treatments and time ($F_{6,28}$=2.75, P=0.05). Despite removing individuals while sampling the predator exclusion treatment, *O. insidiosus* increased throughout the experiment and was significantly higher in this treatment compared with the large-mesh treatment (P=0.027) by July 29 (Figure 2.6).

## Discussion

Generalist predators can exert strong top-down population regulation of *A. glycines* in soybean fields (Costamagna and Landis 2007a). *Harmonia axyridis* is one of the most abundant predators found in soybean across the invasive range of *A. glycines* (Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2007a), thus understanding its role in shaping the *A. glycines* predator guild is of critical importance in the overall suppression of this invasive species.

### *Microcosm studies*

In microcosm experiments we found that *H. axyridis* acting as both an intraguild and a direct predator had differential impacts on both the survival of the intraguild prey and *A. glycines* population dynamics. In tests with *A. aphidimyza*, the presence of this predator alone slowed, but did not prevent, the eventual increase of *A. glycines* to high levels. Based on this result and the aphid consumption rate data we conclude that under the conditions tested, *A. aphidimyza* was not efficient enough in preventing the aphid from reaching outbreak levels. In contrast, only 3 h of feeding by *H. axyridis* provided suppression of *A. glycines* essentially equal to the continuous presence of *A. aphidimyza* over the full 168 h. During its 3 h tenure, *H. axyridis* also acted as a significant intraguild predator of *A. aphidimyza*. This IGP did not result in a release of aphid populations from overall control; aphid populations exposed to both predators were not significantly different from aphids exposed only to *A. aphidimyza*. The overall picture that emerges from this experiment is that while *H. axyridis* is an intraguild predator of *A. aphidimyza*, IGP did not release *A. glycines* from control as *A. aphidimyza* is simply not efficient enough at the densities tested to suppress the aphid on its own.

A somewhat different picture emerges for the *C. carnea* and *H. axyridis* interaction. As in the previous experiment, *H. axyridis* alone slowed but did not prevent the eventual increase of *A. glycines* to high levels. However, in contrast to *A. aphidimyza*, *C. carnea* larvae alone were able to maintain *A. glycines* populations at low levels throughout the experiment. IGP of an effective predator could potentially release aphids from control. While *H. axyridis* did significantly reduce *C. carnea*, it did not reduce the levels of this intraguild prey to the same degree as it did *A. aphidimyza*. This may be because *C. carnea* are larger, more mobile, or less preferred intraguild prey than *A. aphidimyza*. The overall result was that either *C. carnea* alone or the combination of *C. carnea* and *H. axyridis* together resulted in experiment-long aphid control.

Taken together, the microcosm experiments illustrate a complex set of interactions between *H. axyridis*, *A. aphidimyza*, *C. carnea* and *A. glycines*. First, even a single visit by a *H. axyridis* may produce long term impacts on aphid suppression. Three hours of *H. axyridis* feeding significantly reduced overall *A. glycines* population growth in both experiments. In the field, a similar result could mean a difference of several days in when a threshold population is reached or could conceivably even maintain aphid populations below thresholds, particularly if repeated visits by transient coccinellid predators occur. Second, intraguild predators can have strong or weak impacts on intraguild prey depending on their ability to exploit particular guild members and the intraguild prey's ability to escape predation. Third, the ability of *A. aphidimyza* and *C. carnea* to suppress aphid populations after IGP depends on both the number which survive and their inherent ability to consume prey. Finally, it is likely that relatively stochastic events such as the exact timing of intraguild interactions and the numbers of all predators and prey will shift the outcome of these interactions.

*Field cages*

In the field cage experiment aphid populations were reduced in cages, allowing colonization by *H. axyridis* and *C. septempunctata*. Predation by coccinellids delayed *A. glycines* from reaching the 250 per plant threshold for 2 wks compared with the medium-mesh and predator exclusion treatments. Throughout this investigation numbers of all predators remained low in all treatments, indicating that small numbers of predators can have a significant impact on *A. glycines* populations in the field. We were unable to exclude *O. insidiosus* from our predator exclusion treatment; its abundance was highest in this treatment by the end of the experiment. These data indicate that *O. insidiosus* may have benefited from the exclusion of other predators; however, it appears to have little impact on aphid biological control when acting alone at the population levels found in this experiment. While *A. aphidimyza* larvae were more abundant and lacewing larvae were only found in the medium-mesh treatment, there was not a significant difference in the number of these intraguild prey between the medium- and large-mesh treatments. Since IGP did occur in our microcosm experiments, it is likely to also occur at some level in the field. It is possible that the confined arena of a microcosm elevated the extent of IGP relative to what occurs in soybean fields. Alternatively, the relatively low and variable number of *A. aphidimyza* and *C. carnea* found in our field study may have reduced our ability to detect differences. Coccinellid larvae were more abundant in the large-mesh treatment and *H. axyridis* was the most common species. Since *H. axyridis* and *C. septempunctata* were able to deposit eggs inside the large-mesh cage treatment, larvae would not have to colonize these cages. This could have led to higher populations in this treatment compared to the medium-mesh where coccinellid larvae would have to disperse into the cages on their own. Coccinellid larvae are likely to greatly impact both IGP and aphid population dynamics. Aphid consumption by *H. axyridis* can vary from 90 to 370 aphids (depending on the species of aphid) during its larval stage (Hukusima and Kamei 1970 in Koch 2003). Coccinellid larvae are also known to act as intraguild predators (Lucus et al 1998, Kajita et al. 2000, Snyder et al. 2004 a, b). It is likely that in this study coccinellid larvae contributed to decreased aphid populations in the large-mesh treatment and may have engaged in intraguild interactions with other predators.

When evaluating our field cage experiment, it is critical to assess the role of cage design in influencing the results. Our primary concern was that our predator exclusion cages prevented dispersal of alate aphids, which could have been responsible for the elevated aphid populations in this treatment. While a lack of alate dispersal may have contributed to higher *A. glycines* populations, there is evidence that this is not the only factor resulting in lower populations in the large-mesh cage treatment. If dispersal was driving the difference in aphid abundance, the medium-mesh and large-mesh treatments should have both had significantly fewer aphids, as alates could disperse from these treatments. Instead, we found that the number of aphids in the medium-mesh which allowed alate dispersal did not differ from populations in the exclusion treatment where dispersal was prevented. This indicates that it was the difference between the large-mesh and medium-mesh treatments that resulted in better aphid suppression. The only difference between these treatments was the presence or absence of *H. axyridis* and *C.*

*septempunctata*. A second concern was that our medium-mesh was small enough to exclude large lady beetles but still provided equal colonization of small predators compared with the large-mesh treatment. We evaluated this in a preliminary greenhouse experiment prior to conducting our field experiment. We established two portable hoop-houses on top of a greenhouse bench and inside each placed one medium-mesh cage and one large-mesh cage. Inside each cage were 12 heavily-infested soybean plants. The cages was surrounded on all sides with 2 rows of uninfested soybean plants onto which we released *O. insidiosus* adults, *A. aphidimyza* adults and *C. carnea* larvae (100 individuals of each species). The cages were sampled at 48 hr, 96 hr, and 144 hr after the release of the predators. For both *O. insidiosus* ($F_{1,2}$=1.84, P=0.779).and *C. carnea* ($F_{1,2}$=0.07, P=0.817) there was no difference in colonization across the three sampling periods. As adult *A. aphidimyza* were released we did not begin to detect larvae until 96 h, when one larva was found in a large-mesh cage. At 144 h there was not a significant difference in colonization by *A. aphidimyza* in the medium-mesh and large-mesh treatments ($F_{1,2}$=2.13, P=0.281). Our third concern was that abiotic conditions were equal in all cages. To prevent greater shading in our predator exclusion treatment we used the exclusion mesh for the roofs of all three cage treatments, so that all treatments were equally shaded.

### *Impacts of H. axyridis on biological control*

The impact of guild member displacement by an intraguild predator in overall biological control of aphids is likely to depend on several factors, including the contribution of each natural enemy to aphid suppression and the severity of the IGP. The benefit of an intraguild predator such as a lady beetle to overall biological control may be tied to its foraging strategy. Rosenheim and Corbett (2003) modeled how foraging strategy can impact the outcome of biological control of a sedentary pest. They found that when the top predator exhibited a sit and wait foraging strategy, actively foraging intermediate predators were suppressed, releasing sedentary herbivore populations from overall control. This outcome changed when the top predator was an active forager, as is the case with *H. axyridis*. Here the sedentary herbivore was not released from overall control because both the intermediate and top predators were likely to encounter and consume it, so any losses of intermediate predators due to IGP had less of a direct effect on pest suppression (Rosenheim and Corbett 2003). This is what we find in the soybean system, where biological control of the sedentary *A. glycines* was not impacted by the removal of *A. aphidimyza* and *C. carnea* by the active top predator *H. axyridis*.

While adult coccinellids are often significant intraguild predators (Colunga-Garcia and Gage 1998, Losey and Denno 1998, Lucas et al. 1998, Phoofolo and Obrycki 1998, Cardinale et al. 2003, Colfer et al. 2003, Snyder et al. 2004b, Snyder et al. 2004a, Cottrell 2005), inclusion of these predators often results in increased biological control (Colfer and Rosenheim 2001, Cardinale et al. 2003, Aquilino et al. 2005). The presence of *H. axyridis* has been found to increase biological control of aphid pests in communities containing other predators as well as predators and parasitoids. Aquilino et al. (2005) manipulated the diversity of host plant species and predators in microcosms to determine how top-down and bottom-up diversity affected consumption of pea aphid, *Acyrthosiphon pisum* Harris. They found that increasing the diversity of predators increased aphid consumption. This was attributed to poor performance of *Nabis* sp. and *C. maculata* when each predator was present alone. In contrast, consumption by *H.*

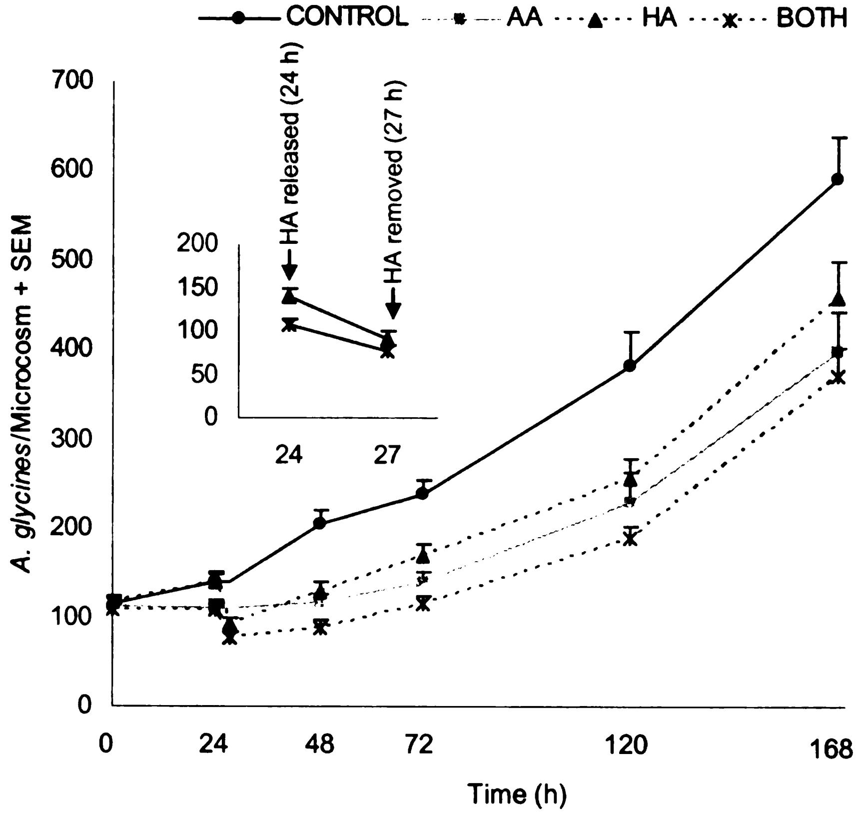
*axyridis* alone in the majority of treatments was typically equal to or exceeded consumption in microcosms containing all three predators (Aquilino et al. 2005). Cardinale et al. (2003) found that when *H. axyridis*, *Nabis* sp., and the parasitic wasp *Aphidius ervi* Haliday were combined in field cages greater pea aphids suppression than was predicted by the summed impact of each species alone (Cardinale et al. 2003). Snyder et al. (2004a) found that on caged rose plants infested with *Macrosiphum euphorbiae* Thomas, the presence of *H. axyridis* dampened aphid populations without impacting the density of *Aphelinus asychis* (Walker) pupae. Similarly, in soybean Costamagna (2006) found that although high levels of IGP of parasitoids by predators were detected, no evidence for disruption in the level of parasitism was found. In contrast, the presence of coccinellids, including *H. axyridis*, was responsible for strong suppression of *A. glycines* and restored soybean biomass and yield to levels similar to control treatments lacking aphids (Costamagna 2006).

### *Conclusions*

My hypothesis was that early in the season when lady beetles are highly mobile, IGP events occurring between the exotic coccinellid *H. axyridis* and larvae of the native *C. carnea* and *A. aphidimyza* could impact the success of soybean aphid biological control. While the transient top predator *H. axyridis* did act as an intraguild predator of both intermediate predators *A. aphidimyza* and *C. carnea*, we did not find evidence of a release of soybean aphid due to IGP in either our microcosm or field cage experiments. Based on the results of this study, the presence of *H. axyridis* may contribute to local declines in *A. aphidimyza* and *C. carnea*; however, biological control of soybean aphid would not likely be improved by removing *H. axyridis* from the system. When *H.*

*axyridis* is excluded from aphid colonies in the field, populations grow to levels not significantly different from cages excluding all predators. This suggests that intraguild prey in the soybean system, including *A. aphidimyza*, *C. carnea*, and *O. insidiosus*, while important to native biological diversity, are not currently major contributors to overall biological control of this invasive pest.

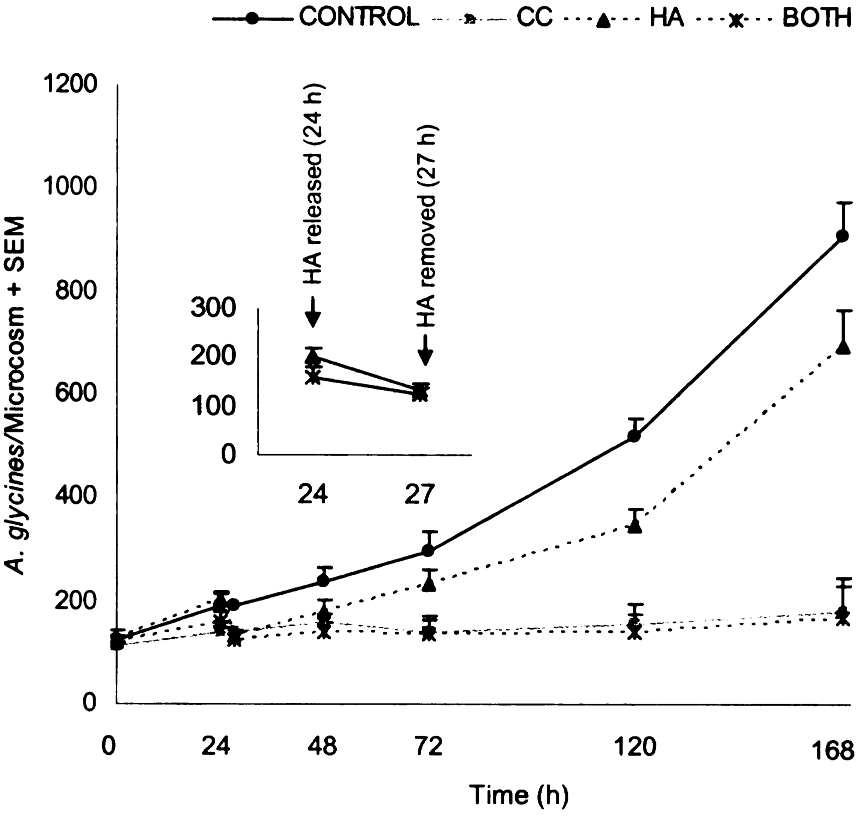
Figure 2.1.



| TREATMENT | 0 | 24 | 27 | 48 | 72 | 120 | 168 |
|---|---|---|---|---|---|---|---|
| CONTROL | a | a | - | a | a | a | a |
| AA | a | a | - | bc | bc | bc | c |
| HA | a | a | a | b | b | b | b |
| BOTH | a | a | a | c | c | c | c |

Figure 2.1. Mean number of *A. glycines* per microcosm in the CONTROL (*A. glycines* only), AA (*A. glycines* + *A. aphidimyza*), HA (*A. glycines* + *H. axyridis*) and BOTH (*A. glycines* + *A. aphidimyza* + *H. axyridis*) treatments. Larval *A. aphidimyza* were released at 0 h, *H. axyridis* were released at 24 h and removed at 27 h. Only the BOTH and HA treatments (which included *H. axyridis*) were counted at 27 h. The figure insert shows the change in aphid populations after 3 h of feeding by *H. axyridis* in the HA and BOTH treatments. Mean comparisons are based on square-root transformed data ($P<0.05$).

Figure 2.2.



| TREATMENT | 0 | 24 | 27 | 48 | 72 | 120 | 168 |
|---|---|---|---|---|---|---|---|
| CONTROL | a | ab | - | a | a | a | a |
| AA | a | a | - | b | b | c | c |
| HA | a | b | a | ab | a | b | b |
| BOTH | a | ab | a | b | b | c | c |

Figure 2.2. Mean number of aphids per microcosm in the CONTROL (*A. glycines* only), CC (*A. glycines* + *C. carnea*), HA (*A. glycines* + *H. axyridis*) and BOTH (*A. glycines* + *C. carnea* + *H. axyridis*) treatments. Larval *C. carnea* were released at 0 h, *H. axyridis* were released at 24 h and removed at 27 h. Only the BOTH and HA treatments (which included *H. axyridis*) were counted at 27 h. The figure insert shows the change in aphid populations after 3 h of feeding by *H. axyridis* in the HA and BOTH treatments. Mean comparisons are based on square-root transformed data ($P<0.05$).

Figure 2.3.

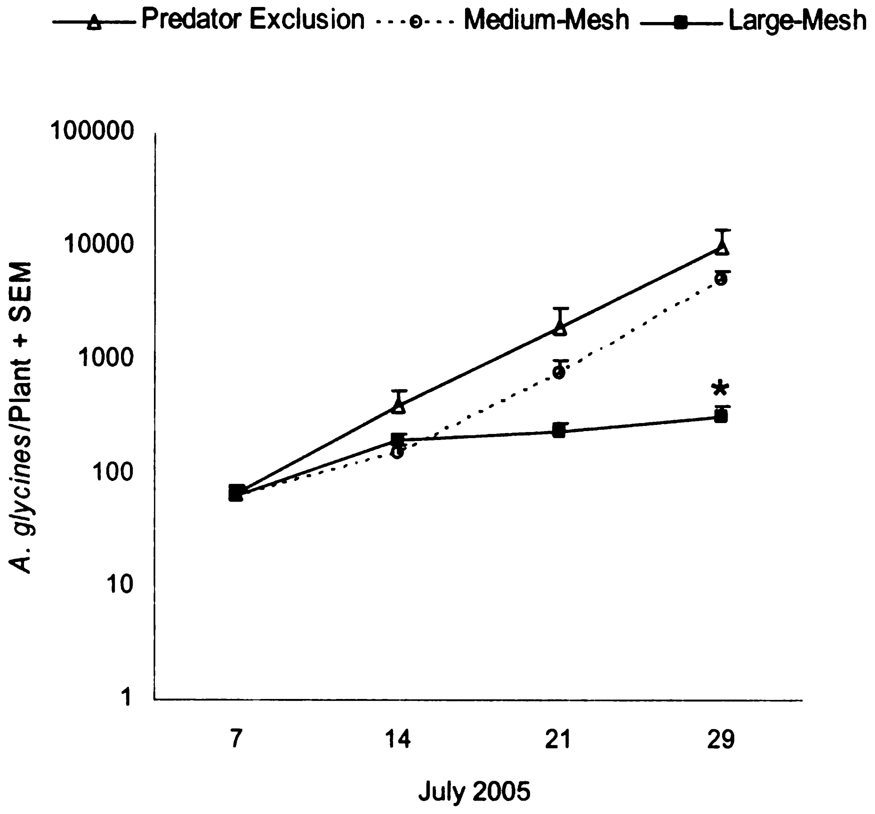


Figure 2.3. Mean number of *A. glycines* per plant in predator exclusion, medium-mesh (small predators only) and large-mesh (small and large predators) cage treatments. Asterisk indicates a significant difference between square-root transformed mean *A. glycines* in the predator exclusion and large-mesh treatments ($P<0.05$).

Figure 2.4.

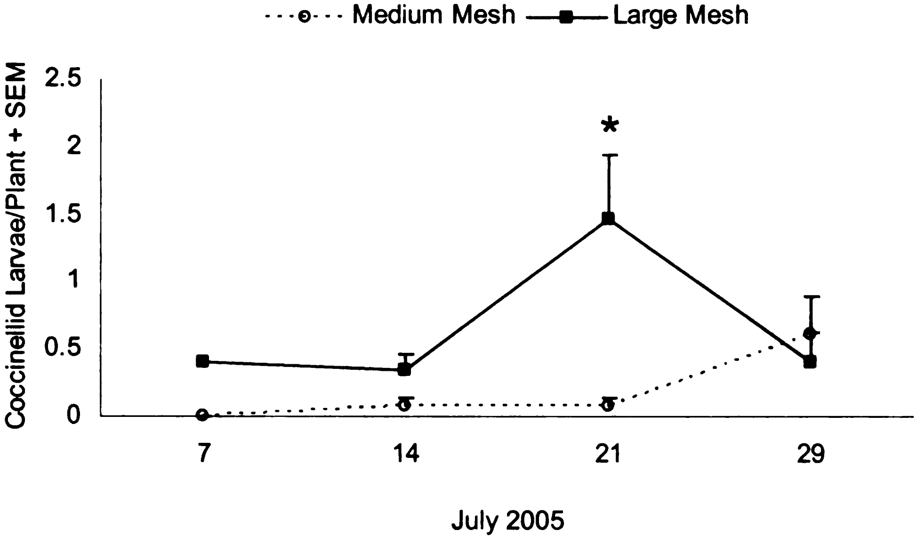


Figure 2.4. Mean number of lady beetle larvae per plant in the medium-mesh and large-mesh cage treatments. Asterisk indicates a significant difference between treatments based on square-root transformed data (*P*<0.05).

Figure 2.5.

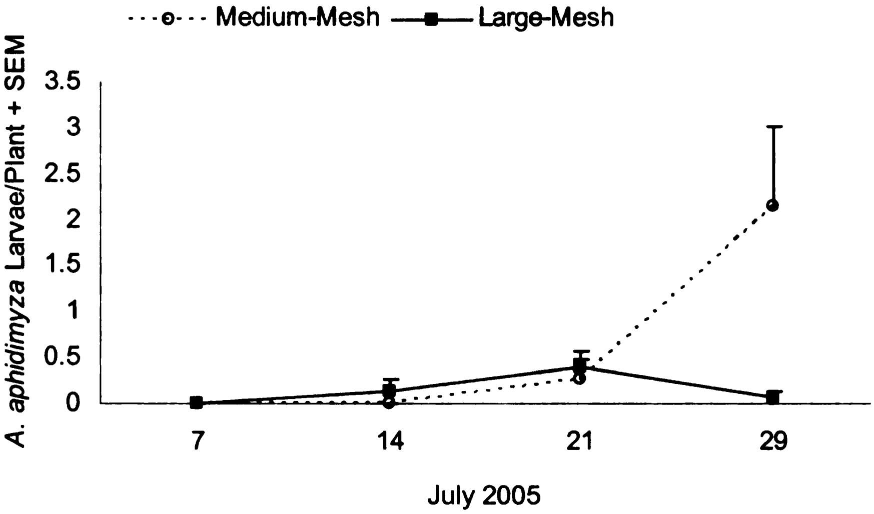


Figure 2.5. Mean number of *A. aphidimyza* per plant in medium-mesh and large-mesh cage treatments.

Figure 2.6.

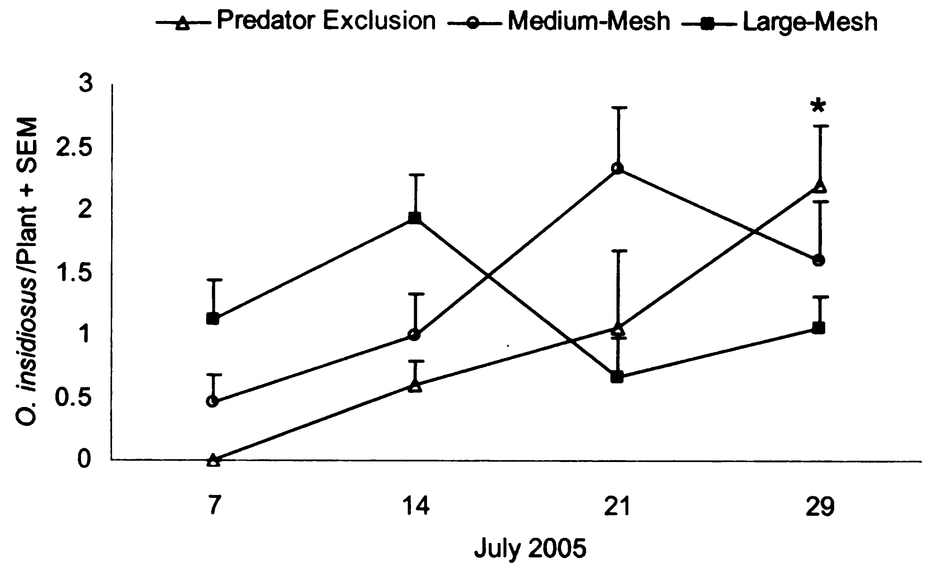


Figure 2.6. Mean number of *O. insidiosus* per plant in the predator exclusion, medium-mesh and large-mesh treatments. Asterisk indicates a significant difference between the predator exclusion and large-mesh treatments based on square-root transformed data ($P<0.05$).

# CHAPTER 3

# LANDSCAPE DIVERSITY ENHANCES BIOLOGICAL CONTROL OF AN INTRODUCED CROP PEST IN THE NORTH-CENTRAL U.S.

## Abstract

Arthropod predators and parasitoids provide valuable ecosystem services in agricultural crops by suppressing populations of insect herbivores. Many natural enemies are influenced by non-crop habitat surrounding agricultural fields and understanding if, and at what scales, land use patterns influence natural enemies is essential to predicting how landscape alters biological control services. Here I focus on biological control of soybean aphid, *Aphis glycines* Matumura, a specialist crop pest recently introduced to the north-central U.S. I measured the amount of biological control service supplied to soybean in 26 replicate fields across Michigan, Wisconsin, Iowa, and Minnesota across two years (2005-06). I measured the impact of natural enemies by experimentally excluding or allowing access to soybean aphid infested plants and comparing aphid population growth over 14 d. I also monitored aphid and natural enemy populations at large in each field. Predators, principally coccinellid beetles, dominated the natural enemy community of soybean in both years. In the absence of aphid predators, *A. glycines* increased significantly, with 5.3 fold higher aphid populations on plants in exclusion cages versus the open field after 14 d. I calculated a biological control services index (BSI) based on relative suppression of aphid populations and related it to landscape diversity and composition at multiple spatial scales surrounding each site. I found that BSI values increased with landscape diversity, measured as Simpson's D. Landscapes dominated by corn and soybean fields provided less biocontrol service to soybean compared with landscapes with an abundance of crop and non-crop habitats. The abundance of Coccinellidae was related to landscape composition, with beetles being more abundant in landscapes with an abundance of forest and grassland compared with landscapes dominated by agricultural crops. Landscape diversity and composition at a scale of 1.5 km surrounding the focal field explained the greatest proportion of the variation in BSI and Coccinellidae abundance. This study indicates that natural enemies provide a regionally important ecosystem service by suppressing a key soybean pest, reducing the need for insecticide applications. Furthermore, it suggests that management to maintain or enhance landscape diversity has the potential to stabilize or increase biocontrol services.

## Introduction

Insects provide vital ecosystem services including decomposition, pollination, and biological control of crop pests (Losey and Vaughan 2006). In agroecosystems, the diversity and abundance of natural enemies that provide biological control in crop fields are influenced by the structure and composition of the surrounding landscape (Marino and Landis 1996, Colunga-Garcia et al. 1997, Bommarco 1998, Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharntke 2005, Tscharntke et al. 2005b). Landscape variables such as habitat complexity, quality, and patchiness as well as an organism's dispersal capability all impact the ability of a landscape to support biological control in agricultural croplands (Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharntke 2005). Moreover, agricultural crop fields are ephemeral habitats in which anthropogenic disturbances such as tillage, pesticide application, and harvesting require arthropods to frequently re-colonize crops (Wissinger 1997). The surrounding landscape provides the local species pool of arthropods for this re-colonization and thus may influence the level of biological control in frequently disturbed crop fields (Lee et al. 2001).

Invasions of exotic species can significantly alter the abundance and distribution of herbivores within a landscape. Landscapes vary in their suitability for invasive species, and understanding how landscape structure influences pest suppression is critical to successfully managing invaders in their non-native range. In the summer of 2000, the soybean aphid, *Aphis glycines* Matsumura, was first detected in the U.S., and has now spread throughout 23 soybean growing states and 3 Canadian provinces (Venette and Ragsdale 2004). Feeding by *A. glycines* on the leaves, stems, and pods of the soybean plant causes reductions in photosynthetic rate (Macedo et al. 2003), plant growth, and seed yield of soybean plants (Ragsdale et al. 2007). Soybean aphid is consumed by a diversity of natural enemies that can provide strong top down regulation of its populations (Costamagna and Landis 2007a) and result in a trophic cascade of increased crop yields (Costamagna et al. 2007a). While several parasitoids can be found attacking soybean aphid, generalist predators currently dominate the natural enemy community (Costamagna et al. *in press*).

A complex of native and exotic generalist predators attack and feed on soybean aphid in North America. These include *Harmonia axyridis* Pallas, *Coccinella septempuncata* L., *Hippodamia variegata* (Goeze), *Hippodamia convergens* Guérin-Méneville, and *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae), *Orius insidiosus* Say (Hemiptera: Anthocoridae), *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), *Aphidoletes aphidomyza* (Rondani) (Diptera: Cecidomyiidae), *Leucopis* spp. (Diptera: Chamaemyiidae), and Syrphidae (Diptera) (Fox et al. 2004, 2005, Desneux et al. 2006, Costamagna and Landis 2007a). Generalist predators have been shown to significantly reduce soybean aphid populations (Fox et al. 2005, Desneux et al. 2006, Costamagna and Landis 2007a), however, the level of suppression is not consistent between studies. For example, Desneux (2006) reported low overall aphid populations (less than 10 per plant) varying only 1.1-3.5 fold in the presence/absence of predators. In contrast, Costamagna and Landis (2007a) reported aphid populations of several thousand per plant varying 6.8 fold in the presence/absence of predators. These studies were conducted in landscapes that vary tremendously in complexity, from diverse landscapes in Michigan (Fox et al. 2004, Costamagna and Landis 2007a) to corn and soybean-dominated landscapes in Indiana (Desneux et al. 2006). It is likely that differences in the efficacy of biological control are due to variation in landscape composition surrounding soybean fields across the north central region.

Given strong local variation in the level of soybean aphid suppression, the goal of this study was to determine if and at what scales, landscape diversity and composition may explain biological control of *A. glycines* in agricultural landscapes. My hypothesis was that landscapes composed of a high proportion of non-crop habitat such as grasslands and forests would provide overwintering habitat and alternative prey resources to natural enemies. Such landscapes would in turn increase the abundance of generalist predators and result in greater suppression of the soybean aphid. My objectives were to 1) measure the impact of predator assemblages on soybean aphid populations across the north central U.S. and 2) determine if the level of biological control detected in soybean fields was related to the diversity and composition of the surrounding landscape.

## Methods

### *Field sites*

Between June and August of 2005 and 2006, I examined the abundance of aphids and arthropod natural enemies at 26 sites distributed amongst 4 states (Iowa, Michigan, Minnesota, and Wisconsin) in the north-central U.S. as part of a larger multi-state study of soybean aphid management (Figure 3.1). Sites were selected to study how landscape variation across a large portion of the soybean growing region affected biological control of soybean aphid. Within each year, a minimum distance of 30 km separated each field site. Across years, I maintained the relative regional distribution of sites, but sampled different fields. The average distance between soybean fields sampled in subsequent years was 1.6 km (range = 0.2-4.6 km, Figure 3.1). Field size averaged 16.0 ha (range = 13.6-48.1 ha). In each replicate field, a randomized complete block design with 4-6 blocks and either 4 (2005) or 5 (2006) treatments was established in 0.4 ha (2005) or 0.2 ha (2006) plots. Multiple experiments occurred within these fields, and this study was conducted in plots which were not treated with insecticide.

### *Natural enemy impact experimental design*

Following the methods of Costamagna et al. (2007a), I used cages to exclude natural enemies from selected plants, contrasting the population growth of aphids in the presence or absence of these antagonists. When an average population of 10 aphids per plant was reached in the overall field, a cage were erected in the center of each plot (4 per site), each enclosing a single plant. Each caged plant was paired with an un-caged plant, 1 m away in the same row, hereafter referred to as "open" plants. Aphids were either added or removed to start each plant with 10 aphids of mixed age classes. In some locations, aphid populations never reached an average level of 10 aphids per plant. In these sites I manually redistributed aphids from the field to the experimental plants to initiate the study. Cages consisted of a 0.4 m diameter x 1 m tall tomato wire support covered by a sleeve of fine-mesh white no-see-um netting (openings of 0.65 x 0.17 mm; Kaplan Simon, Braintree, MA). The mesh sleeve was tied at the top and attached to a metal "T" post, it was secured at the bottom by burying the edges in the soil. The number of apterous and alate aphids was recorded weekly on both the open and caged plants using non-destructive field counts 7 and 14 d post establishment.

*Assessment of cage effects*

Cage studies must address possible effects on microclimate and test organism behavior. Using similar cages, Costamagna and Landis (2007a) found that a "sham" cage treatment (exclusion cages with windows to allow access by natural enemies) and a no-cage treatments did not differ significantly in aphid population growth after 7 or 14 d. Another potential concern is that exclusion cages could prevent dispersal of alate aphids and artificially elevate aphid populations. To minimize this possibility, I limited our study to 14 d. After 7 d, alate number was low and similar (1.4 ± 0.1 and 1.9 ± 0.1 alate aphids per plant (mean ± SEM)) in the exclusion cage and open treatments respectively. At 14 d the exclusion cage treatment had an average of 20.7 ± 1.4 alates per plant while the open plant had 1.8 ± 0.1 alates per plant. To examine the impact of cages with a high number of alates on our results, I analyzed a sub-set of the data excluding all cages which had more alates than were found on open plants (10% of cages). Exclusion of these data from analysis (not shown) did not affect the outcome.

### *Soybean aphid and natural enemy sampling*

Destructive whole plant counts were used to estimate *A. glycines* abundance at weekly intervals from early June until late August. In each plot, 5 randomly selected plants were removed from the ground and the number of apterous and alate aphids were counted on each plant. I present the date of first aphid detection and the date when the economic threshold of 250 aphids per plant (Ragsdale et al. 2007) was reached for each site (Table 3.1).

During the two weeks of the natural enemy impact experiment, the diversity and abundance of natural enemies was estimated using two different sampling techniques (Schmidt et al. 2008b). To measure aerially dispersing natural enemy populations, a single unbaited yellow sticky card (PHEROCON AM, Great Lakes IPM, Vestaburg, MI) was placed in each plot at all study sites. In the center of each plot, a metal "T" fence post was erected with holes every 10 cm vertically. A 0.6 cm diameter dowel was placed through a hole to suspend a 22.9 x 27.9 cm sticky card just above the plant canopy. Sticky traps were collected at 7 and 14 d and all adult Coccinellidae, Anthocoridae, Nabidae, Chrysopidae, Hemerobiidae and Syrphidae (2006 only) were counted. I also visually inspected plants on day 7 and 14 to measure the diversity and abundance of natural enemies foraging in soybean. In 2005, five randomly selected plants were inspected per plot and all adult and immature Coccinellidae, *Orius insidiosus* (Anthocoridae), Nabidae, Chrysopidae, Hemerobiidae, Syrphidae, *Aphidoletes aphidimyza* (Cecidomyiidae), Araneae, Aphelinidae, and Braconidae were counted. In 2006, I reduced the number of locations sampled by visual plant counts to one site per state and inspected 10 randomly selected plants per plot.

*Landscape analysis*

Field geospatial data was collected using a handheld GPS receiver using Wide Area Augmentation System (WAAS) correction. The spatial coordinate for the center of each site was used to obtain ortho-rectified digital aerial imagery. I digitized the habitats surrounding each study site to a radius of 3.5 km using ARC GIS 9.1. These aerial images differed temporally, representing images captured between 1998 and 2006. Land use changes between the image date and study period were recorded by ground-verification in June – August annually, with corrections made during the digitization process. At the same time I also determined the specific land cover present within all areas of each landscape (Table 3.2). Some locations included polygons that were not visible from a roadway and permission to access private lands could not be obtained. These polygons were given a value of zero and were excluded from further analysis. The area of each site that could not be identified varied from 0-2%. The smallest polygons identified included field plots on university research farms and small patches of fallow field ($< 5\ m^2$) the largest were contiguous urban areas, lakes, and forests ($< 11.9\ km^2$).

Landscape diversity was measured using Simpson's Index (D) (Simpson 1949). Simpson’s Index is typically used to examine the variance of species abundance distributions, here I applied it to examine variance in the proportion of area covered by each of 22 landuse categories. This index was calculated for each of the landscapes at each of the spatial scales examined. The equation for Simpson’s Index (D) is: $D = 1/\sum(pi)^2$ where pi=proportion of habitat in the $i^{th}$ land-cover category (D increases as diversity increases). Using methods modeled after Thies et al. (2003) I measured landscape diversity at 7 spatial scales ranging from 0.5 km to 3.5 km radii (at 0.5 km intervals) from the field center.

*Statistical analysis*

A repeated-measures mixed model analyses of variance (ANOVA) (PROC MIXED in SAS v. 9.1) was used to compare the average aphid populations on the caged and open plants in the 26 locations sampled. Fixed factors included in the model were: cage treatment, week, and the cage treatment*week interaction. Cage treatment replicate nested within site was included as a random effect and week was the repeated variable. Differences in aphid abundance between treatments were assessed by comparing least squares means. Aphid counts were log transformed prior to analysis to meet the assumptions of normality and homogeneity of variances (SAS Institute, 1999).

To relate biological control services to landscape variables I calculated the relative aphid suppression found in each site by expressing the change in aphid numbers on open and caged plants, as a proportion of aphid abundance in the absence of predators for any given site. The resulting Biocontrol Services Index (BSI), varied from 0-1, with values increasing as the level of aphid predation increases.

$$BSI = \frac{\left( \sum_{p=1}^{4} \frac{\left( Ac_p - Ao_p \right)}{Ac_p} \right)}{n}$$

Where Ac = the number of aphids on the caged plant on day 14, Ao= the number of aphids on the open plant on day 14, p=plot, and n= the number of replicates for a given site. In one case a negative BSI value was calculated due to higher aphid populations on the open plant than in the corresponding exclusion cage treatment. Since this indicated a lack of effective biological control, this site was given an index value of zero.

To evaluate the relationship between predator abundance, BSI, and landscape variables, I performed a principal components analysis (PCA). The 22 land use categories were combined into 8 variables included in the PCA analysis: 4 crop variables (proportion corn, soybean, wheat and other crops), and 4 non-crop variables (proportion forest, grasslands, urban, and water) (Table 3.2). Principal component axes were extracted using the correlations among variables and the resulting factors were not rotated. I restricted our analysis to the first two eigenvectors which together explained between 43.8-56.1% of the variability in landscape data. This was done for each spatial scale (radii of 0.5–3.5 km). The PCA analysis was completed using JMP version 7 (SAS Institute 2007).

To assess the influence of the principal components and landscape diversity (D) on BSI and coccinellid abundance (the average number of adult Coccinellidae collected from sticky cards across the two weeks of sampling) I compared all possible models containing these variables using Akaike's Information Criterion, adjusted for sample size (AICc) (Burnham and Anderson 2002). The AICc analysis was conducted at each spatial scale of analysis (0.5-3.5 km). At radii of 1 km and larger, eight models were compared: Intercept only, Diversity (Simpson's D), PC1, PC2, Diversity + PC1, Diversity + PC2, PC1 + PC2, and Diversity + PC1 + PC2. At a 0.5 km radius the interpretation of PC2 was not consistent with larger spatial scales and was not included in model analysis. For each analysis, I present the maximum log-likelihood estimate, the Akaike weights ($W_i$) and AICc differences ($\Delta_i$). For each response variable I present the model with the minimum AICc value, which has the best support for the data and any other models with a AICc difference of less than 2 (Burnham and Anderson 2002). Models with a $\Delta_i$ in this range are termed "competing models" (Ribic and Sample 2001) and are considered to also have substantial support for the data (Burnham and Anderson 2002). I calculated adjusted $r^2$ for the minimum AICc model and competing models to evaluate how well the models explained the variation in the data. I also calculated partial correlations for all variables in models with more than one predictor. Partial correlations were used to assess the importance of individual independent variables after adjusting for additional variables in the model. The AICc analysis and adjusted $r^2$ were determined using R version 2.1.1 (R Development Core Team 2005). Partial correlations were obtained using PROC CANCORR in SAS v. 9.1 (SAS Institute 1999). Three sites were excluded from this analysis. In 2005, only the 7 d count was collected at site 2 and 9, therefore BSI values could not be calculated for these sites. In 2006, ground-verification of the landscape data was not collected for site 25 (Figure 3.1).

Sites that are geographically close may be more similar than sites that are farther apart (Legendre 1993). Therefore, before interpreting the results of our AIC analysis for either BSI or Coccinellidae abundance, I determined if the residuals from the best fit or competing models were spatially autocorrelated by examining sample variogram plots. For both response variables I did not detect spatial autocorrelation among the 23 sites.

## Results

### *Aphid populations in 2005 and 2006*

In 2005, *A. glycines* arrival in soybean was detected beginning in mid-June in Michigan, Minnesota, and Wisconsin. Soybean aphid was detected about one month later in the Iowa sites, beginning on July 7 (Table 3.1). Of the 12 sites sampled, 8 reached the economic threshold of 250 *A. glycines* per plant in the field as a whole. The date at which threshold was reached in the field at large varied from mid-July to late-August (Table 3.1). Populations in exclusion cages exceeded threshold in 11 of 12 sites on average 11.6 days earlier than the open field. In 2006 soybean aphid was detected beginning in mid-June through mid-July in all sites except site 25 in Iowa where aphids were not found until August 10. Only two of the 14 sites reached threshold in the field at large while in exclusion cages eight sites exceeded threshold (Table 3.1).

### *Predator and parasitoid diversity across the region*

Coccinellidae, Syrphidae, Chrysopidae, and Anthocoridae were the most abundant predators collected on sticky cards (Figure 3.2). Nine species of coccinellids were observed. Across the region, *H. axyridis* comprised the greatest proportion of the coccinellid population in both years (70% in 2005, 72% in 2006). Visual plant counts illustrated that Coccinellidae and Anthocoridae were the most abundant natural enemies found on soybean plants (Figure 3.2). The most abundant lady beetle species found on soybean plants was *H. axyridis,* with adults and larvae comprising 47 and 88% of the coccinellid community in 2005 and 2006. Anthocoridae consisted solely of adult and nymphal *O. insidiosus*.

### *Impact of predators on soybean aphid*

Despite their apparent low abundance, natural enemies had a large impact on soybean aphid, with significantly higher aphid populations occurring on caged versus open plant treatments. The relationship between these treatments across the two weeks of the experiment varied as indicated by a significant cage treatment*week interaction ($F_{1,44}$=9.36, *P*=0.003, Figure 3.3). However, the open treatment was significantly lower than the exclusion cage both 7 (*P*=0.002) and 14 (*P*<0.0001) d after establishment.

### *Landscape diversity*

The landscape surrounding each of our field sites varied from agriculturally-dominated to forest and grassland-dominated. Within the 3.5 km landscape radius surrounding each of the 23 sites, landscape diversity values (D) ranged from 2.43-6.40. Landscapes with low D values were dominated by corn and soybean fields while landscapes with high D values included a diversity of crop and non-crop habitats. The percentage of the landscape composed of annual cropland ranged from 20-91%. Landscapes with low to high percentages of annual cropland were found within each state (Michigan 20-91%, Wisconsin 29-71%, Minnesota 44-73%, and Iowa 27-89%). Soybean and corn production covered between 4-38% and 9-57% of the 3.5 km landscape respectively. The percentage of the landscape composed of forested habitat ranged from 1-42%.

### *Interpretation of principal components*

Both principal components were interpreted as measures of landscape composition. Sites with positive loadings on PC1 were correlated with forested land cover while sites with negative loading values were correlated with corn and soybean. Positive values of PC1 suggest a landscape dominated by forested habitats while negative values of PC1 indicate a landscape dominated by corn and soybean agriculture (Figure 3.4). The interpretation of PC2 is scale dependent, with the correlation of the factor loadings consistent only at scales of 1 km and greater. Here positive scores were correlated with the variables other crops and wheat indicating that landscapes with high loadings had a high proportion of locally important fruit, vegetable and ornamental and small grain crops. Negative values were correlated with the variables grassland and water, indicating landscapes with a high proportion of these more permanent habitat types. (Figure 3.4).

*Model comparisons*

Overall, BSI was best predicted by the Simpson's D at a spatial scale of 1.5 km (Table 3.3) having the lowest AICc score of any model at the 7 spatial scales examined. The Simpson's D model was also the best predictor of BSI at 1, 2, 2.5 and 3 km while the PC1 model had the lowest AICc scores at both 0.5 and 3.5 km. Competing models included Diversity + PC1, Diversity + PC2, and PC1 (Table 3.3). There was a significant positive relationship between BSI and landscape diversity, indicating that the degree of soybean aphid suppression by natural enemies increased as diversity of crop and non-crop habitats in the surrounding landscape increased (Figure 3.5).

Overall Coccinellidae abundance was best predicted by the PC1 + PC2 model at a spatial scale of 1.5 km (Table 3.5). This model had the lowest AICc value and contained 43% of Akaike weight. The abundance of coccinellids was positively correlated with PC1 and negatively correlated with PC2 indicating that these predators were most abundant in soybean field in landscapes dominated by forests and to a lesser extent, grasslands (Figure 3.6). Competing models at 1.5 km included Diversity+PC1+PC2, and Diversity+PC1. The Diversity and Diversity+PC2 models had the lowest AIC value at 0.5 and 1.0 km respectively while the PC1 model had the lowest AICc at spatial scales of 2 km and greater.

## Discussion

Biological control of pests is an important yet infrequently measured ecosystem service (Swinton et al. 2006). In this study, I found that the ability of a landscape to supply biocontrol services as manifested by suppression of the soybean aphid was a function of the diversity of the agricultural landscape, and that coccinellids, the primary predator of soybean aphid, responded to the presence of natural habitat within the landscape.

*Impact of biological control*

Previous authors have illustrated the importance of natural enemies in the suppression of aphid populations at the field scale (Dennis and Wratten 1991, Grasswitz and Burts 1995, Rutledge et al. 2004, Schmidt et al. 2004, Muller et al. 2005, Gardiner and Landis 2007). Schmidt et al. (2004) found the exclusion of flying natural enemies led to 94% higher populations of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.). Similarly, Fox et al. (2004), Costamagna and Landis (2007a), Costamagna and Landis (2007a) Desneux (2006), and Donaldson et al. (2007) found that a diverse generalist natural enemy complex significantly reduced soybean aphid populations in individual soybean fields while parasitoids are currently not major contributors (Costamagna et al. *in press*). Because of its potential for rapid population growth (Costamagna et al. 2007b) predation early in the season is key to preventing aphids from reaching threshold levels. Our study is the first to demonstrate that such phenomena are regionally important and result from the actions of natural enemy communities that vary with landscape composition.

Using exclusion cages, I found that communities of generalist predators are effective at suppressing *A. glycines* populations across a wide portion of the north central U.S. Suppression was found even though soybean production practices, time of first aphid infestation, and plant growth stage all varied widely during the study (Table 3.1).

This reduction was not always effective in maintaining populations below the economic threshold, but without predation, aphid populations exceeded thresholds earlier in the season and more often than in the absence of predators. Since its detection in 2000, the soybean aphid has exhibited apparently cyclic outbreaks, with high populations in one year typically followed by low populations the following year. These cyclic outbreaks are likely attributable to the work of generalist predators which build populations in high aphid years and prevent outbreak populations the following year. I conducted this study in a high (2005) and low (2006) soybean aphid year and found that in both cases predators reduced the proportion of sites that exceeded threshold. Within 14 days, soybean aphid populations exceeded the threshold of 250 aphids per plant in 92% of exclusion cages sampled in 2005 and 57% in 2006, while in the presence of predators this dropped to 67% in 2005 and 14% in 2006, ie. the presence of predators would have reduced the need for insecticide treatment by 25-43% in 2005 and 2006 respectively. Remarkably, this study demonstrates that low numbers of natural enemies are required to achieve this suppression. Through this and other studies (Costamagna and Landis 2007, Costamagna et al. in press) I now understand that small but consistent predation early in the season is they key to preventing aphids from reaching threshold levels.

### *Ability of the landscape to supply biocontrol services*

While I observed a significant impact of biological control across this 4-state region, there was also significant variation in the amount of aphid suppression among sites which was strongly influenced by the diversity of the surrounding landscape. Agricultural landscapes have changed dramatically with agricultural intensification, resulting in larger more contiguous fields and non-crop areas reduced in area and frequency (Bianchi et al. 2006). I found that low diversity landscapes dominated by soybean and corn production had reduced biological control of soybean aphid compared with diverse landscapes dominated by non-crop habitats. In a 2006 review, Bianchi et al. (2006) found that increased landscape complexity reduced pest pressure in 45% of the studies. Effects included reductions in pest density (Ostman et al. 2001, den Belder et al. 2002) and reduction in crop injury (Thies and Tscharntke 1999, Thies et al. 2003). Pest pressure increased with landscape complexity in 15% of the cases examined (Raffy and Tran 2005, Roschewitz et al. 2005) while the two were unrelated in 40% of the studies (Galecka 1966, Holland and Fahrig 2000, Klug 2003, Thies et al. 2005). It is likely that some of this variation is tied to differences in the impact of landscape complexity on specific natural enemy populations. A more detailed understanding of how natural enemies respond to landscape structure may help us understand these outcomes.

### *Response of natural enemies to landscape diversity and composition*

Tscharntke et al. (2005b) addressed the potential impact of agricultural intensification on the disruption of ecosystem services including biological control, stating that simple landscapes may support lower abundance of natural enemies, reduced enemy biodiversity perhaps lacking a key species, or by restricting movement of natural enemies within the landscape. In this study I found that coccinellids were more abundant in soybean fields in landscapes with an abundance of forests and grasslands. These landscapes were more diverse and supported greater biocontrol of soybean aphid as measured by the BSI compared with landscapes dominated by agricultural habitat. Coccinellid species have been shown to be key predators of soybean aphid (Costamagna and Landis 2007a, Gardiner and Landis 2007) as well as other pest aphids. Thus, to promote biological control in agricultural landscapes, it may be desirable to maintain a diversity of these habitats to favor these natural enemies.

The influence of landscape diversity on natural enemies has been addressed in several systems (Bommarco 1998, Elliott et al. 1999, Thies et al. 2003). Predator diversity and abundance typically increase with landscape diversity, proportion of non-crop habitat, and degree of connectedness between non-crop habitat patches, while decreasing with crop field size. For example, Elliott et al. (1999) found that uncultivated land and habitat patchiness were both associated with increasing abundance and richness in predator communities in wheat fields. Similarly, Thies et al. (2003) found that parasitism of the rape pollen beetle was positively correlated with percent non-crop habitat.

*Landscape spatial scale*

In this study, I examined the impact of landscape variables on biological control at 7 spatial scales, with landscape radii varying from 0.5 km to 3.5 km. Analysis of landscape features at a radius of 1.5 surrounding focal soybean fields explained the highest proportion of the variation in both biological control of soybean aphid (BSI) and coccinellid abundance. While I know relatively little about the movement of coccinellids it is possible that a landscape of this size encompasses their ecological neighborhood (Addicott et al. 1987) containing the diversity of habitats utilized by these species. During early summer when aphid populations in croplands are low these predators are likely to be very transient, moving between fields in search of prey. Landscapes of a similar grain size have proved important in predicting both herbivory and natural enemy abundance in other systems. For example, Thies et al. (2003) measured the functional spatial scale at which the rape pollen beetle, *Meligethes aeneus* F. and its parasitoids were affected by landscape. They tested the effects of landscape on trophic-level interactions using simple (<3% non-crop habitat) to complex (>50% non-crop habitat) landscapes, and analyzed them at 8 spatial scales, (concentric circles 0.5-6 km in diameter) and found that herbivory and parasitism were most strongly correlated with percent non-crop area at a diameter of 1.5 km. Schmidt and Tscharntke (2005) found that sheetweb spider abundance in wheat fields was correlated with non-crop area at a slightly larger spatial scale (landscape circles with a radius of 1-3 km).

### *Implications*

This study is the first to demonstrate that the biocontrol service provided by generalist predators in north-central U.S. soybean fields is dependent on the diversity and composition of the surrounding landscape. Biological control of *A. glycines* is reduced in simple landscapes dominated by corn and soybean production. Coccinellidae, an important family of *A. glycines* natural enemies, were also found to decline in soybean fields located in agriculturally-dominated landscapes. Therefore, maintaining overall landscape diversity, and especially perennial grassland and forested habitats in the landscape will favor suppression of soybean aphid. Moreover, these habitats may also enhance biocontrol services in other crops as the generalist natural enemies found in soybean fields are also important antagonists of many other herbivores. Our results suggest that such non-crop habitats do not need to directly border agricultural fields to promote biocontrol services, as I found that occurrence of these habitats within approximately 1.5 km explained the highest proportion of the variation in both biological control and coccinellid abundance.

Finally, understanding the impact of shifting production practices on biocontrol services in agricultural landscapes is of critical importance. For example, in many parts of the north-central U.S. corn and soybean were typically rotated annually. Recently corn acreage is on the rise in response to increased demand for corn ethanol, with harvested acres rising by 15 million acres between 2006 and 2007 (NASS 2008). Increasing pressure to produce biofuel crops on agricultural lands could have a negative effect on biocontrol services in these landscapes particularly if corn production increases, reducing landscape diversity and displacing habitats associated with greater predator abundance. This could have a negative effect on biocontrol services as the pressure to produce biofuels on cropland increases.

Table 3.1. Study sites with dates of first aphid detection, period of predator exclusion cage study, dates when aphid threshold was reached in the open field and exclusion cages, and plant stages during cage study. Simpson's D values are shown for the 1.5 km landscape radius surrounding each soybean field.

| | | | Date | | | | | |
|---|---|---|---|---|---|---|---|---|
| State | Site # | Year | Aphid Detection | Cage Study | Threshold[1] (Field) | Threshold[2] (Exclusion) | Plant Stage[3] | Simpson's D[4] |
| MI | 1 | 2005 | 6/29 | 7/6-7/20 | 7/13 | 7/20 | R2-R3 | 5.42 |
| MI | 2 | 2005 | 6/8 | 7/13-7/20 | 7/20 | 7/13 | R2-R3 | – |
| MI | 3 | 2005 | 6/14 | 6/20-7/5 | 8/1 | 7/5 | V2-V5 | 5.09 |
| MI | 4 | 2005 | 6/14 | 6/20-7/5 | 7/18 | 7/5 | V4-R2 | 6.40 |
| WI | 5 | 2005 | 6/20 | 7/11-7/25 | – | 7/25 | R2-R3 | 3.85 |
| WI | 6 | 2005 | 6/16 | 6/30-7/14 | – | 7/14 | R1-R2 | 3.27 |
| WI | 7 | 2005 | 6/17 | 6/17-7/1 | – | 6/17 | V5-R1 | 3.27 |
| MN | 8 | 2005 | 6/16 | 7/14-7/27 | 7/27 | 7/27 | R2-R3 | 4.22 |
| MN | 9 | 2005 | 6/30 | 7/21-7/28 | 7/28 | – | R2-R3 | – |
| IA | 10 | 2005 | 7/7 | 7/11-7/25 | 8/29 | 7/25 | R2-R4 | 3.24 |
| IA | 11 | 2005 | 7/13 | 7/13-7/28 | – | 7/28 | R2-R3 | 3.51 |
| IA | 12 | 2005 | 7/19 | 7/26-8/10 | 8/16 | 8/10 | R3-R5 | 2.31 |
| MI | 13 | 2006 | 6/14 | 7/6-7/19 | – | 7/19 | R1-R2 | 6.06 |
| MI | 14 | 2006 | 6/19 | 7/31-8/14 | – | 8/14 | R2-R3 | 5.78 |
| MI | 15 | 2006 | 7/13 | 7/19-8/2 | – | 8/2 | R3 | 6.53 |
| MI | 16 | 2006 | 6/19 | 8/7-8/21 | – | 8/21 | R3 | 5.20 |
| WI | 17 | 2006 | 6/29 | 7/20-8/3 | – | – | R3-R5 | 7.06 |
| WI | 18 | 2006 | 6/9 | 7/14-7/28 | – | – | V7-R2 | 2.42 |
| WI | 19 | 2006 | 7/7 | 7/21-8/4 | – | 8/4 | R2-R4 | 3.89 |
| MN | 20 | 2006 | 6/5 | 7/17-7/31 | – | 7/31 | R2-R5 | 2.98 |
| MN | 21 | 2006 | 7/5 | 7/17-7/31 | 7/25 | 7/31 | R2-R3 | 3.41 |
| IA | 22 | 2006 | 6/15 | 7/25-8/8 | – | – | R4-R5 | 3.11 |
| IA | 23 | 2006 | 7/19 | 7/26-8/9 | – | – | R4-R5 | 3.61 |
| IA | 24 | 2006 | 7/10 | 7/24-8/7 | – | 8/7 | R4-R5 | 2.32 |
| IA | 25 | 2006 | 8/10 | 8/10-8/24 | 8/30 | – | R4-R6 | – |
| IA | 26 | 2006 | 7/14 | 8/11-8/25 | – | – | R5-R6 | 2.25 |

[1] Date when overall field exceeded the economic threshold of 250 aphids per plant.

[2] Date when plants in exclusion cages exceeded the economic threshold.

[3] Based on Higley and Boethel (1994)

[4] Simpson's D for 1.5 km radius, $D = 1/\sum(pi)^2$ where pi=proportion habitat in the ith category

Table 3.2. Land cover categories used in the calculation of Simpson's Diversity Index (D) and as variables included in the principal components analysis.

| Simpson's Diversity (D) | PCA |
|---|---|
| Cropland Categories | |
| Corn | Corn |
| Soybean | Soybean |
| Wheat | Wheat |
| Sugar Beet | Other Crops[1] |
| Dry Bean | |
| Tree Fruit | |
| Sunflower | |
| Cabbage | |
| Canola | |
| Potato | |
| Carrot | |
| Squash | |
| Pea | |
| Strawberry | |
| Tilled Field | |
| Ornamental Crops | |
| Non-Crop Categories | |
| Forage | Grassland[2] |
| Old Field and Restored Prairie | |
| Pastureland | |
| Forested | Forest |
| Wetlands and Open Water | Water |
| Urban | Urban |

---

[1] Other Crops contains all Simpson's D cropland categories except corn, soybean, and wheat.

[2] Grassland contains the Simpson's D non-crop categories Forage, Old Field and Restored Prairie, and Pastureland

Table 3.3. Summary of model selection statistics for evaluating predation of *A. glycines* by generalist natural enemies, calculated as a biocontrol services index (BSI) (see methods section 2.6). The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1 2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 0.5 km | $B_0 + B_1\mathrm{PC1}^{\dagger}$ | -3.20 | 3 | 14.07 | 0.00 | 0.53 | 0.16 | |
| 0.5 km | $B_0 + B_1\mathrm{D} + B_2\mathrm{PC1}$ | -2.83 | 4 | 15.88 | 1.82 | 0.21 | 0.14 | D = 0.18, PC1 = 0.40 |
| 1.0 km | $B_0 + B_1\mathrm{D}^{\dagger\dagger}$ | -1.44 | 3 | 11.00 | 0.00 | 0.48 | 0.28 | |
| **1.5 km** | $\boldsymbol{B_0 + B_1\mathrm{D}^{\dagger\dagger}}$ | **-0.89** | **3** | **9.90** | **0.00** | **0.54** | **0.31** | |
| 2.0 km | $B_0 + B_1\mathrm{D}^{\dagger\dagger}$ | -1.60 | 3 | 11.32 | 0.00 | 0.45 | 0.27 | |
| 2.0 km | $B_0 + B_1\mathrm{D}^{\dagger} + B_2\mathrm{PC2}$ | -1.18 | 4 | 13.18 | 1.87 | 0.18 | 0.26 | D = 0.53, PC2 = 0.19 |
| 2.5 km | $B_0 + B_1\mathrm{D}^{\dagger\dagger}$ | -1.86 | 3 | 11.84 | 0.00 | 0.43 | 0.25 | |
| 3.0 km | $B_0 + B_1\mathrm{D}^{\dagger}$ | -2.69 | 3 | 13.50 | 0.00 | 0.28 | 0.19 | |
| 3.0 km | $B_0 + B_1\mathrm{PC1}^{\dagger}$ | -2.73 | 3 | 13.58 | 0.08 | 0.27 | 0.19 | |
| 3.0 km | $B_0 + B_1\mathrm{D} + B_2\mathrm{PC1}$ | -2.08 | 4 | 14.98 | 1.49 | 0.13 | 0.20 | D = 0.23, PC1 = 0.23 |
| 3.5 km | $B_0 + B_1\mathrm{PC1}^{\dagger}$ | -2.05 | 3 | 12.22 | 0.00 | 0.45 | 0.24 | |

[1] D = Simpson's Diversity where $D = 1/\sum(p_i)^2$ and $p_i$=proportion of habitat in the $i^{th}$ land-cover category

[2] $\dagger$ Indicates a variable was significant at $P < 0.05$, $\dagger\dagger$ indicates $P < 0.01$.

Table 3.4. Summary of model selection statistics for evaluating the abundance of Coccinellidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Competing models with a $\Delta_i$ of 2 or less are included.

| Radius (km) | Model$^{1\ 2\ 3}$ | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 0.5 km | $B_0 + B_1D^{\dagger}$ | -33.47 | 3 | 74.61 | 0.00 | 0.43 | 0.19 | |
| 0.5 km | $B_0 + B_1D + B_2PC1$ | -32.49 | 4 | 75.20 | 0.60 | 0.32 | 0.23 | D = 0.41, PC1 = 0.32 |
| 0.5 km | $B_0 + B_1PC1$ | -34.39 | 3 | 76.45 | 1.84 | 0.17 | 0.12 | |
| 1.0 km | $B_0 + B_1D^{\dagger\dagger} + B_2(PC2)^{\dagger\dagger}$ | -30.33 | 4 | 71.48 | 0.00 | 0.39 | 0.35 | D = 0.58, PC2 = -0.54 |
| 1.0 km | $B_0 + B_1PC1^{\dagger\dagger} + B_2(PC2)$ | -30.81 | 4 | 72.44 | 0.96 | 0.24 | 0.32 | PC1 = 0.55, PC2 = -0.39 |
| **1.5 km** | $\boldsymbol{B_0 + B_1PC1^{\dagger\dagger} + B_2(PC2)^{\dagger}}$ | **-30.09** | **4** | **71.00** | **0.00** | **0.43** | **0.36** | **PC1 = 0.56, PC2 = -0.46** |
| 1.5 km | $B_0 + B_1(D) + B_2PC1^{\dagger} + B_3(PC2)$ | -29.47 | 5 | 72.47 | 1.47 | 0.21 | 0.36 | D = -0.23, PC1 = -0.51, PC2 = -0.34 |
| 1.5 km | $B_0 + B_1(D) + B_2PC1^{\dagger\dagger}$ | -30.92 | 4 | 72.66 | 1.66 | 0.19 | 0.32 | D = -0.40, PC1 = 0.60 |
| 2.0 km | $B_0 + B_1PC1^{\dagger\dagger}$ | -32.61 | 3 | 73.34 | 0.00 | 0.30 | 0.24 | |
| 2.0 km | $B_0 + B_1(D) + B_2PC1^{\dagger\dagger}$ | -31.27 | 4 | 73.36 | 0.03 | 0.29 | 0.29 | D = -0.33, PC1 = 0.58 |
| 2.0 km | $B_0 + B_1PC1^{\dagger\dagger} + B_2(PC2)$ | -31.59 | 4 | 74.00 | 0.67 | 0.21 | 0.27 | PC1 = 0.54, PC2 = -0.29 |
| 2.0 km | $B_0 + B_1(D) + B_2PC1^{\dagger\dagger} + B_3(PC2)$ | -30.65 | 5 | 74.83 | 1.49 | 0.14 | 0.30 | D = -0.28, PC1 = 0.56, PC2 = -0.23 |
| 2.5 km | $B_0 + B_1PC1^{\dagger}$ | -32.96 | 3 | 74.04 | 0.00 | 0.43 | 0.22 | |
| 2.5 km | $B_0 + B_1PC1^{\dagger} + B_2(PC2)$ | -32.34 | 4 | 75.50 | 1.47 | 0.21 | 0.22 | PC1 = 0.52, PC2 = -0.23 |
| 2.5 km | $B_0 + B_1(D) + B_2PC1^{\dagger}$ | -32.53 | 4 | 75.88 | 1.85 | 0.17 | 0.21 | D = -0.19, PC1 = 0.49 |
| 3.0 km | $B_0 + B_1PC1^{\dagger}$ | -33.74 | 3 | 75.60 | 0.00 | 0.39 | 0.17 | |
| 3.0 km | $B_0 + B_1PC1^{\dagger} + B_2(PC2)$ | -33.11 | 4 | 77.04 | 1.45 | 0.19 | 0.17 | PC1 = 0.46, PC2 = -0.23 |

Table 3.4 (continued)

| Radius (km) | Model[1 2 3] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 3.5 km | $B_0 + B_1$PC1 | -34.24 | 3 | 76.60 | 0.36 | 0.29 | 0.13 | |
| 3.5 km | $B_0 + B_1$PC1 + $B_2$(PC2) | -33.28 | 4 | 77.38 | 1.15 | 0.19 | 0.16 | PC1 = 0.42, PC2 = -0.28 |
| 3.5 km | $B_0$ | -36.36 | 2 | 78.13 | 1.89 | 0.13 | | |

[1] D = Simpson's Diversity where D = $1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] †Indicates a variable was significant at $P < 0.05$, †† indicates $P < 0.01$

[3] Variables in parentheses indicate a negative relationship with Coccinellidae abundance

Figure 3.1.

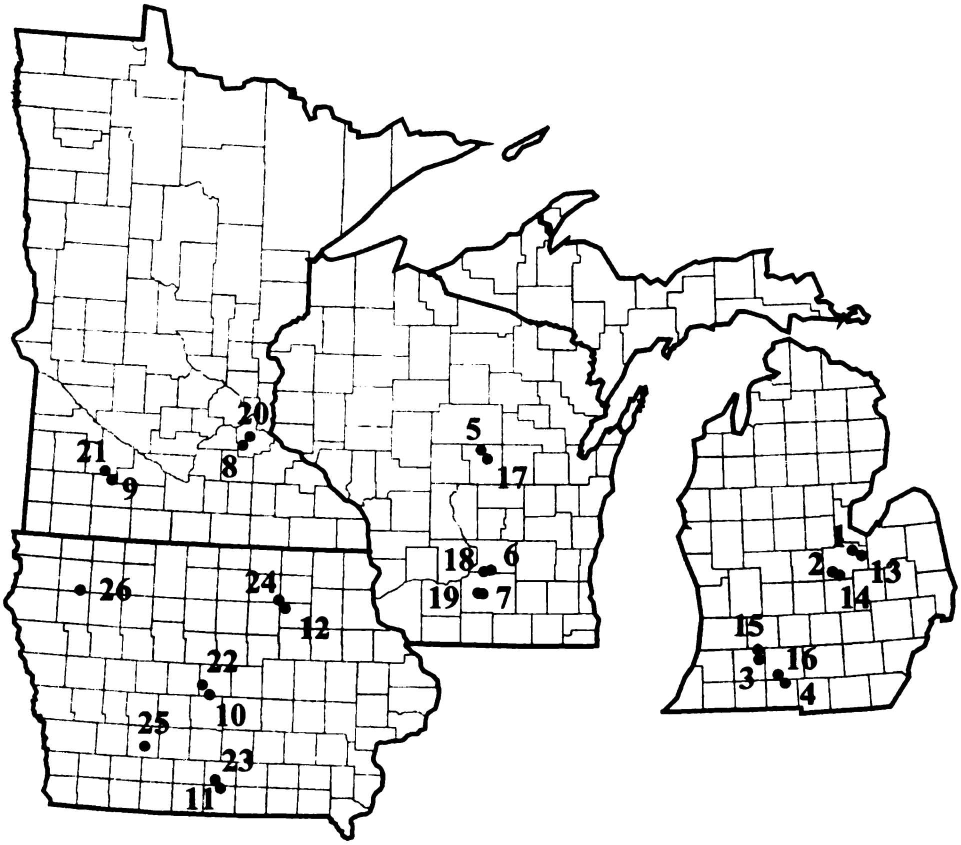


Figure 3.1. Location of 26 soybean fields sampled in 2005 (fields 1-10) and 2006 (fields 11-26). The predator exclusion cage study was completed in all sites. Fields 2, 9, and 25 were excluded from the AICc analysis of BSI and Coccinellidae abundance due to missing data.

Figure 3.2.

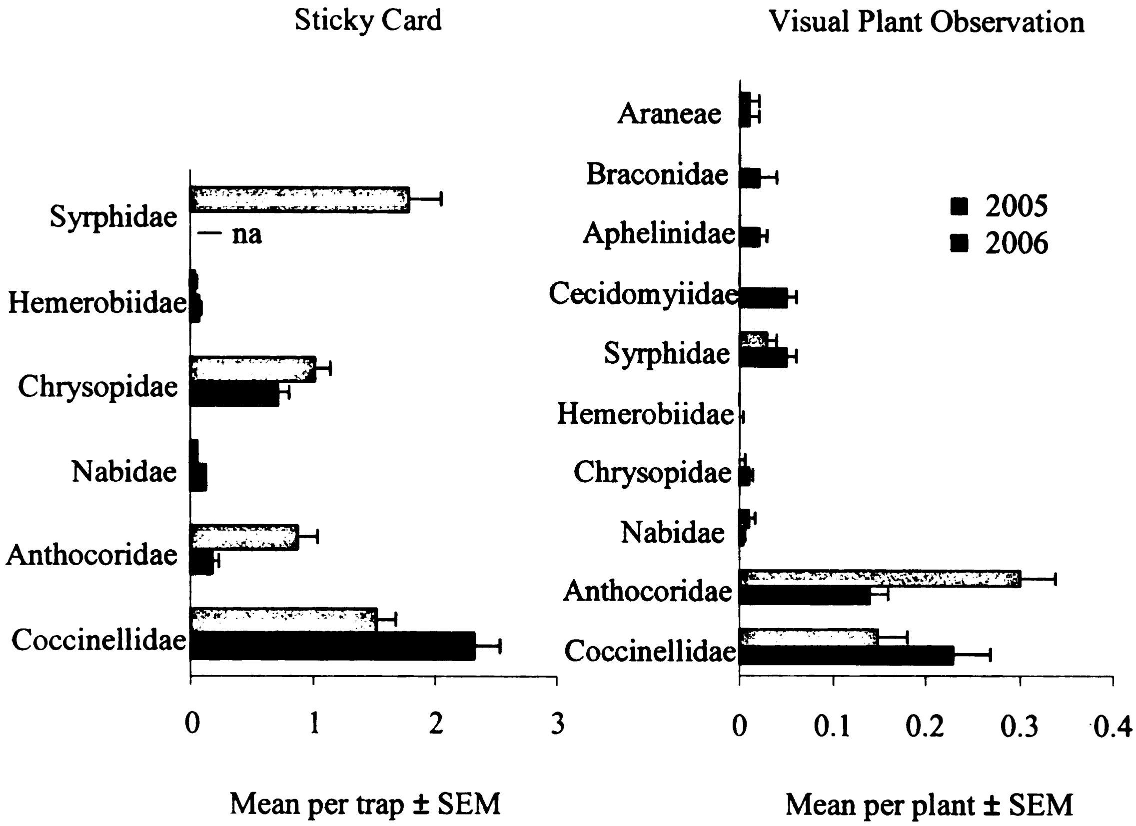


Figure 3.2. Mean number of natural enemies ± SEM counted on sticky card traps (7 d cumulative) and during visual plant observations (illustrates natural enemies present on a plant at a single point in time) in 2005 and 2006. Syrphidae were not counted on sticky cards in 2005.

Figure 3.3.

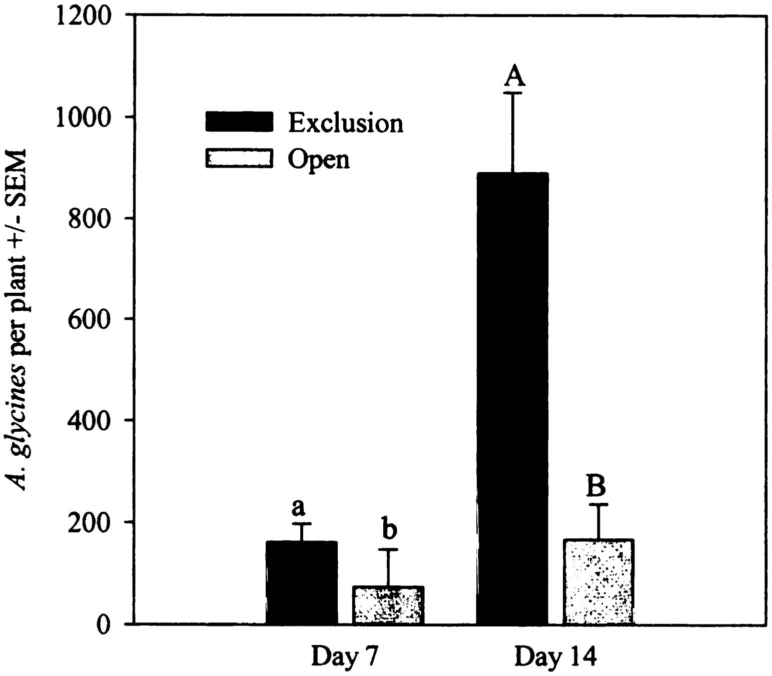


Figure 3.3. Mean number of *A. glycines* per plant (± SEM) in the cage and open plant treatments. A significant week*treatment interaction was found ($F_{1,44}$=9.36, *P*=0.003). Comparison of least squares means at 7 (*P*=0.002) and 14 d (*P*<0.0001) indicates that aphid populations were significantly higher in the absence of natural enemies.

Figure 3.4.

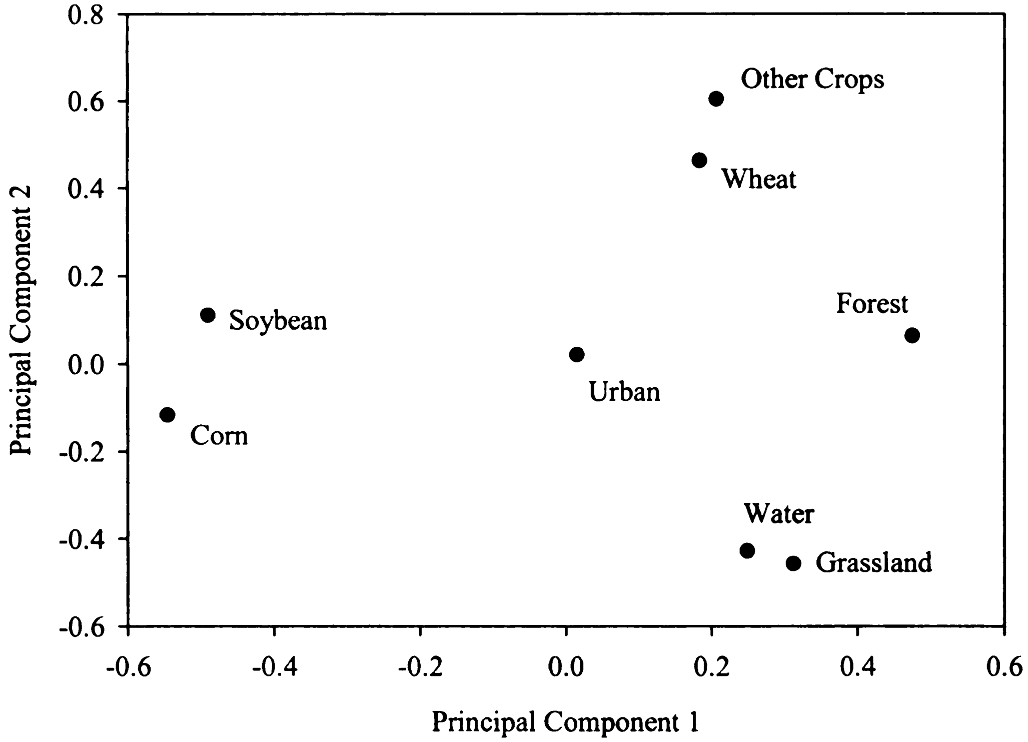


Figure 3.4. PCA ordination for principal components 1 and 2 of landscape elements surrounding soybean fields sampled at a radius of 1.5 km.

Figure 3.5.

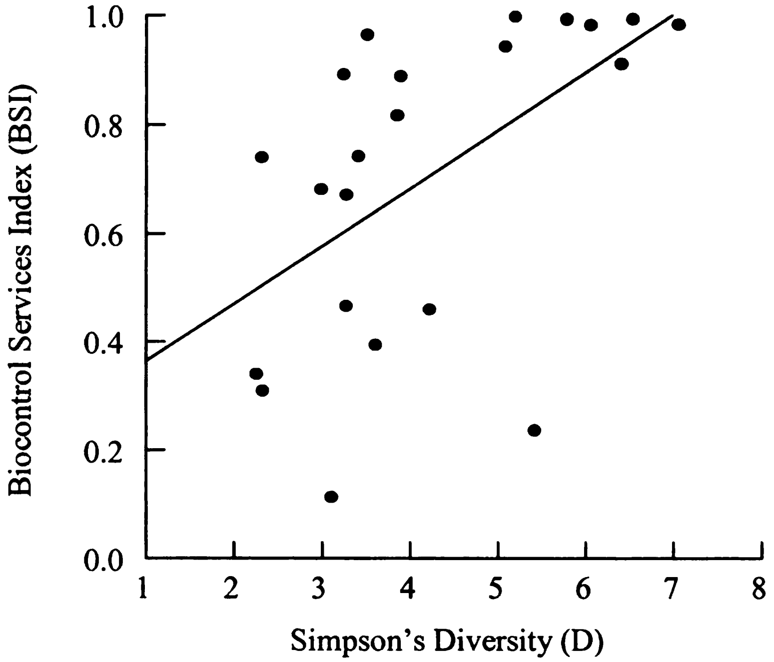


Figure 3.5. Relationship between the biocontrol services index (BSI) and PC1 at a radius of 1.5 km for 23 fields sampled for soybean aphid suppression, 2005-06 ($y = 0.124x + 0.159$). BSI was calculated as the relative difference in aphid number between open and exclusion cage treatments (see methods section 2.6).

Figure 3.6.

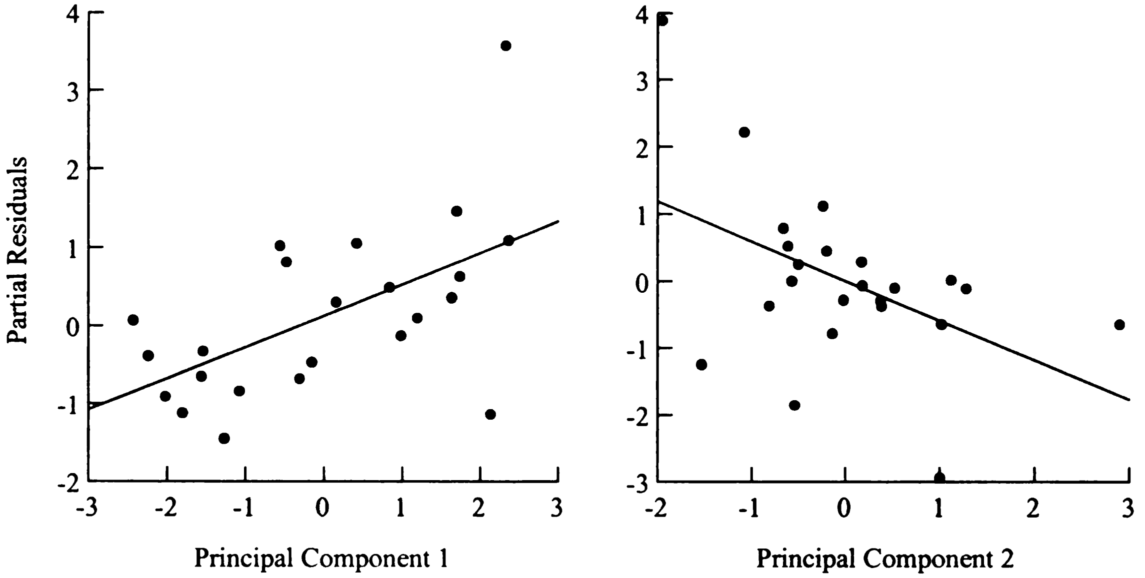


Figure 3.6. Coccinellidae abundance in 23 soybean fields sampled for soybean aphid suppression was best explained by a model containing both PC1 and PC2 at a radius of 1.5 km. ($y = 0.392x_1 - 0.361x_2 + 2.0638$). Partial residual plots illustrate a positive correlation with PC1 and a negative correlation with PC2, indicating that landscapes with an abundance of forests or grasslands support larger lady beetle populations in soybean fields compared with agriculturally-dominated landscapes.

# CHAPTER 4

# LANDSCAPE COMPOSITION INFLUENCES THE ACTIVITY DENSITY OF CARABIDAE AND ARANAE COMMUNITES IN SOYBEAN FIELDS.

## Abstract

The distribution and abundance of semi-natural and agricultural habitats within the landscape is likely to greatly influence landscape-scale metapopulation dynamics of habitat generalists. I investigated the influence of landscape diversity and composition on the activity density of Carabidae, Araneae, and Opiliones. Although I hypothesized each taxa would increase with landscape diversity and the amount of semi-natural habitat, I found variation in the response of the study organisms. The activity density of Araneae supported my hypothesis, increasing in soybean fields in landscapes with an abundance of forests and grasslands. Relationships with Carabidae activity density varied, with adult overwintering and predatory species increasing and larval overwintering species declining with the abundance of grassland in the landscape. Opiliones activity density was not related to the structure of the surrounding landscape at any of the spatial scales examined. The spatial scale at which each taxa responded to landscape composition increased with their capacity for dispersal. Carabidae, which generally disperse by walking, responded to smaller spatial scales than linyphiid spiders, which frequently balloon. These data illustrate the importance of understanding species-specific relationships to landscape variables.

## Introduction

Agricultural landscapes support a diverse metacommunity of ground-dwelling arthropod natural enemies, frequently dominated by Carabidae and Araneae. Many of these natural enemies are habitat generalists and spatial processes play an important role in their metacommunity dynamics and influence interactions between multiple populations linked via dispersal (Liebold et al. 2004, Schmidt et al. 2008). Whereas habitat specialists may exist in patches that effectively function as islands, habitat generalists utilize a mosaic of crop and semi-natural habitats (Schmidt et al. 2008). Wissinger (1997) suggested that natural enemies that immigrate to agricultural fields colonize crops under favorable conditions and retreat to semi-natural habitats when conditions become hostile. Given this dispersal between habitats within a metacommunity, the diversity and abundance of these natural enemies available for biological control in croplands is likely to depend on the large-scale structure of the landscape matrix.

Several patterns have emerged from the study of landscape influences on natural enemy populations. In many cases the diversity, abundance, reproductive success, and biocontrol service provided by natural enemies increases as landscape diversity and the proportion of semi-natural habitat increases (Colunga-Garcia et al. 1997, Fahrig and Jonsen 1998, Elliott et al. 1998, Bommarco 1998), whereas pest number and damage decline (den Belder et al. 2002, Ostman 2002, Thies et al. 2003). For example, spider species richness and the abundance of linyphiid spiders in croplands increased with the proportion of non-crop habitat in the landscape (Schmidt and Tscharntke 2005, Schimidt et al. 2005). Bommarco and Ekbom (2000) report that the fecundity of predatory carabids beetles increased with landscape heterogeneity and with the proportion of perennial crops in the landscape due to higher arthropod abundance and diversity. In addition, Gardiner et al. (2008) found that the biocontrol service supplied to soybean fields and the abundance of coccinellid predators were positively related to the diversity of the surrounding landscape.

In addition, thresholds in landscape structure may exist below which the search efficiency and the ability of natural enemies to aggregate and control pests is diminished (With and King 1999, Wiens et al. 1997, With et al. 1999, Thies and Tscharntke 1999). Simulation and field experiments have shown that biological control by natural enemies declined when suitable habitat fell below 20% (With and King 1999, Thies and Tscharntke 1999). For example, Thies et al. (2003) found that in these simple landscapes, parasitism of rape pollen beetle declined below threshold levels need for successful biological control.

Finally, landscape complexity does not influence all species equally, or at the same scale (Thies et al. 2003, Den Belder et al. 2002, Steffan-Dewenter et al. 2002, Schmidt et al. 2005). Gardiner et al. (in review) found that native and exotic coccinellid populations in soybean responded differently to landscape composition. Native species were more abundant in landscapes with an abundance of grassland while exotic species were most abundant in forest dominated landscapes. Scale of analysis is also critical in interpreting landscape patterns (Thies et al. 2003, Gardiner et al. 2008). Species that are able to fly long distances may survive in a landscape with a smaller number of highly dispersed fragments of suitable habitat, whereas species with a more limited dispersal capacity would not. Therefore, the arrangement and size of suitable habitat patches within a landscape are likely to have species-specific impacts on the activity of habitat generalists in agricultural croplands.

Across much of the north-central U.S., corn and soybean fields form the landscape matrix, which is defined as the most extensive and connected habitat present (Turner et al. 2001). This matrix contains patches of semi-natural habitats including woodlots, grasslands, wetlands and open water. Several studies have related the diversity and abundance of ground beetles and arable spiders in agricultural fields to the composition of the surrounding landscape. However, the majority of these studies have focused on wheat and were conducted in Europe where the matrix structure is much different from that of intensive agricultural areas of the U.S.

My objective was to examine how the activity density of habitat generalist predators is influenced by the amount of semi-natural habitat patches within an agricultural matrix in the north-central U.S. Here I examine three taxa: Carabidae, Araneae, and Opiliones in soybean as part of a larger study on the influence of landscape structure on the suppression of soybean aphid by its natural enemies. Due to the intense disturbance regime present in annual cropping systems, my hypotheses were that: (1) the activity density of Carabidae, Araneae, and Opiliones would increase with the proportion of semi-natural habitats in the landscape, (2) the trophic level and overwintering phenology of a species would affect its response to landscape composition, with predatory species that overwinter as adults having stronger correlations with semi-natural habitat, and (3) the spatial scale at which specific organisms respond to landscape structure, is positively related to its dispersal capacity. Therefore, those that disperse mainly by walking would have a smaller ecological neighborhood compared with groups known to frequently utilize flight or ballooning. I relate the patterns found herein to studies conducted in Europe and in other U.S. cropping systems.

## Methods

### *Field sites*

Between June and August of 2005 and 2006, I examined the activity density of Carabidae, Opiliones and Araneae in 26 soybean fields in Iowa, Michigan, Minnesota, and Wisconsin (Figure 4.1). Sites were selected to study how landscape variation affected the diversity and abundance of these arthropods, as part of a USDA Risk Avoidance and Mitigation (RAMP) funded multi-state study of soybean aphid management. Each year, a minimum distance of 30 km separated each field site. Across years, I maintained the relative regional distribution of our sites, but sampled different soybean fields. The average distance between soybean fields sampled in 2005 and 2006 within a given region was 2.4 km (range = 0.2-14.6 km, Figure 4.1). Field size averaged 16.0 ha (range = 13.6-48.1 ha). In each RAMP field (22 sites), a randomized complete block design with 4-6 blocks and either 4 (2005) or 5 (2006) treatments was established in 0.4 ha (2005) or 0.2 ha (2006) plots. Multiple experiments occurred within these fields; with this study conducted in control plots not treated with insecticide. An additional 4 commercial production fields (2 in 2005 and 2 in 2006) were also included in this study, each containing four 0.4 ha (2005) or 0.2 ha (2006) untreated plots.

### *Pitfall sampling*

Carabidae, Araneae, and Opiliones were collected from each plot using pitfall traps. One pitfall trap was placed within a soybean row in the center of each plot. The trap consisted of a 1000 ml plastic cup with a 11.5 cm diameter opening. Cups were buried at ground level and filled with approximately 500 ml of a 50% propylene glycol solution. Each trap was covered with a rain shield constructed from a 0.9 $m^2$ section of corrugated plastic sheeting and four 0.46 m wire legs. Traps were checked weekly and all Carabidae, Araneae, and Opiliones were collected and identified. All Carabidae and Lycosidae were identified to species (Lindroth 1968, Kaston 1948). The remaining Araneae were identified to family (Ubick 2007). Opiliones were identified to order.

*Landscape analysis*

Field geospatial data were collected using a handheld GPS receiver using Wide Area Augmentation System (WAAS) correction. The spatial coordinate for the center of each site was used to obtain ortho-rectified digital aerial imagery. I digitized the habitats surrounding each study site to a radius of 3.5 km using ARC GIS 9.1. Aerial images were captured between 1998 and 2006. Land use changes between the image date and study period were recorded by ground-verification in June – August annually, with corrections made during the digitization process. At the same time, I also determined the specific land cover (n = 21 categories) present in all areas of each landscape (Table 4.1). Some locations included polygons that were not visible from a roadway and permission to access private lands could not always be obtained. These polygons were given a value of zero and were excluded from further analysis. The area of each site that could not be identified varied from 0-2%. The smallest polygons identified included field plots on university research farms and small patches of fallow field (< 5 $m^2$); the largest were contiguous urban areas, lakes, and forests (< 11.9 $km^2$).

Landscape diversity was measured using Simpson's Index (D) (Simpson 1949). Simpson's Index is typically used to examine the variance of species abundance distributions. Here I applied it to examine variance in the proportion of area covered by each of 21 land use categories. This index was calculated for each of the landscapes at each of the spatial scales examined. The equation for Simpson's Index (D) is: $D = 1/\sum(p_i)^2$ where $p_i$=proportion of habitat in the $i^{th}$ land-cover category (D increases as diversity increases). Using methods modeled after Thies et al. (2003) I measured landscape diversity at 6 spatial scales ranging from 1 km to 3.5 km radii (at 0.5 km intervals) from the field center.

*Statistical analysis*

To evaluate the relationship between activity density and landscape variables, I performed a principal components analysis (PCA) on the landscape variables in order to reduce the dimensions of the data. The 21 observed land cover categories were combined into seven variables included in the PCA: four crop variables (proportion corn, soybean, wheat and other crops), and four non-crop variables (proportion forest, grasslands, wetlands and water, and urban) (Table 4.1). Principal component axes were extracted using correlations among variables and the resulting factors were not rotated (McCune and Mefford 1999). I restricted the analysis to the first two eigenvectors which explained between 53.2-57.1% of the variability in landscape data. This was done for each spatial scale (1.0-3.5 km radii).

To assess the influence of interpreted principal components and Simpson's D on the activity density of Carabidae, Opiliones and Araneae I compared all possible models containing these variables using Akaike's Information Criterion, adjusted for a small sample size (AICc) (Burnham and Anderson 2002). At each spatial scale 7 models were considered (Table 4.2). For each analysis, I present the maximum log-likelihood estimate, the Akaike weights, which estimate the relative likelihood of a given model against all other models, and AICc differences ($\Delta_i$). At each spatial scale I present the model with the minimum AICc value, i.e. with the best support for the data, and any competing models with a AICc difference of less than two (Ribic and Sample 2001, Burnham and Anderson 2002). I calculated an adjusted $r^2$ for the minimum AICc model and competing models to evaluate how well the models explained the variation in the data. I define the best overall model as the model with the lowest AICc score across all spatial scales. I calculated partial correlations for all variables in models with more than one predictor. Partial correlations were used to assess the importance of individual independent variables after adjusting for additional variables in the model. The AICc analysis and adjusted $r^2$ were determined using R version 2.1.1 (R Development Core Team 2005). Partial correlations were obtained using PROC CANCORR in SAS v. 9.1 (SAS Institute 1999). All Carabidae variables and Opiliones were log (x+1) transformed, and the mean number of Araneae and Lycosidae were square root (x+0.5) transformed prior to analysis to meet the assumptions of normality and homogeneity of variances (SAS Institute, 1999).

Although no site had an overlapping 3.5 km landscape buffer within a given year, sites did have overlapping buffers across years. Therefore, prior to interpreting the results of the AICc analysis, I examined potential spatial autocorrelation of the residuals of the best fit and competing models for each response variable between each site and the nearest neighboring site using Moran's I statistic. I did not find evidence of spatial autocorrelation between neighboring sites for any of the best fit models for any response variable.

## Results

*Activity density in soybean fields*

A total of 29,300 ground beetle individuals comprising 62 species were collected from 26 soybean fields in 2005 or 2006 across the 4-state study region (Table 4.3). The majority of these species were predators or omnivores (91.6%) that overwintered as larvae (56%) (Table 4.3). Overall, the most abundant species was *Cyclotrachelus sodalis* (LeConte), which was most abundant in soybean during late June to early July followed by *Poecilus chalcites* (Say) which was most abundant in from mid June to mid July (Figure 4.2). Other abundant species included (in order of abudance): *Pterostichus permundus* (Say), *Harpalus pensylvanicus* (DeGeer), *Harpalus eraticus* Say, *Poecilus lucublandus* (Say), *Scarites quadriceps* Chaudior and *Pterostichus melanarius* (Illiger) (Table 4.4 and Figure 4.2). The proportional distribution of species varied across the 4 states sampled. Whereas *C. sodalis* was the most abundant species in Iowa (51.1% of total) and Minnesota (58.5%), *P. calcites* (61.4%) and *H. erraticus* (46.4%) were the most abundant species collected in Michigan and Wisconsin respectively. Among all taxa samped these was considerable variation in abundance from year to year (Figure 4.2).

A total of 3,215 Araneae and 9,058 Opiliones were collected in pitfall traps. In both 2005 and 2006 Araneae activity density peaked in late June. Eight families were found; Lycosidae was the most abundant followed by Linyphiidae (Table 4.5, Figure 4.3). Nine species of Lycosidae were collected, the most abundant were *Trochosa terricola* Thorell and *Pardosa saxatilis* (Hentz) (Table 4.5, Figure 4.4).

*Landscape diversity*

The landscape surrounding each of our field sites varied from agriculturally-dominated, to forest and grassland-dominated. Within the 3.5 km landscape radius surrounding each of the 26 sites, landscape diversity values (D) ranged from 2.43-6.40. The percentage of the landscape composed of annual cropland ranged from 19-91%. Landscapes with high and low percentages of annual cropland were sampled in each state (Michigan 19- 91%, Wisconsin 29-71%, Minnesota 44-84%, and Iowa 27-89%). At a 3.5 km radius grassland habitat comprised 1-69% (Michigan 3-19%, Wisconsin 4-20%, Minnesota 6-19%, and Iowa 5-69%) while forested habitat comprised 0-42% of the landscape surrounding field sites (Michigan 3-32%, Wisconsin 3-42%, Minnesota <1-16%, and Iowa 0-6%)

### *Principal component analysis of landscape variables*

Both of the principal components interpreted in this study were measures of landscape composition (Figure 4.5). Sites with positive loadings on PC1 were correlated with the variable Forest while negatives loadings on PC1 were correlated with the variables Corn and Soybean. Therefore sites with positive values of PC1 suggest a landscape with an abundance of wooded habitat while sites with negative values of PC1 indicate a landscape dominated by corn and soybean agriculture (Figure 4.5). For PC2, sites with positive loadings were correlated with the variable Grassland and negative loadings were correlated with the variables Other Crops and Wheat. Sites with high values of PC2 had a high proportion of pastures, old fields, and restored prairies. Sites with negative values had a high proportion of locally important fruit, vegetable, ornamental and small grain crops (Figure 4.5). Both principal components indicate the intensity of landscape disturbance, with high values indicating less disturbed grassland and forested habitats and low values indicating greater agricultural disturbance.

*Relationships between activity density and landscape variables*

The activity density of Carabidae was best predicted by the PC2 model at all 6 spatial scales examined; the PC2 model at a 1 km radius had the lowest AIC value across scales (Table 4.6). The PC1 + PC2 and intercept only were competing models. A marginally significant negative correlation was detected between Carabidae and PC2 ($P = 0.04$, $r^2=0.13$), indicating that activity density was reduced in soybean fields surrounded by an abundance of grasslands compared to landscapes dominated by regionally important crops and wheat (Figure 4.6).

*Adult-overwintering species*

When ground beetles were analyzed by overwintering stage, differences were found in their response to landscape variables. The activity density of ground beetles overwintering as adults was best predicted by the PC2 model at all spatial scales except a radius of 2.5 km where the full model PC1+PC2+Diversity had the lowest AIC value (Table 4.7). The PC2 model at a radius of 1 km had the lowest AIC value across scales. Competing models included PC2, PC1 + PC2, PC2 + D, and PC1 + PC2 + D. Adult-overwintering beetles were significantly negatively correlated with PC2 ($P < 0.0001$, $r^2 = 0.57$), indicating that their activity density in soybean fields was greater in landscapes with an abundance of wheat and regionally important crops compared with landscapes dominated by grassland (Figure 4.6). The most abundant adult-overwintering species collected was *P. calcites*. Like adult-overwintering beetles as a whole, the activity density of *P. calcites* in soybean declined with the abundance of grassland in the landscape (*P* = 0.02, $r^2$ = 0.21) (Figure 4.6).

### *Larval-overwintering species*

The activity density of ground beetles overwintering as larvae was also best predicted by the PC2 model at all spatial scales; the PC2 model at a radius of 2.5 km had the lowest overall AICc value (Table 4.8). Unlike adult-overwintering beetles, the activity density of larval overwintering species was significantly positively correlated with PC2 (*P* = 0.01, $r^2$ = 0.23). The activity density of these species increased in soybean fields in landscapes surrounded by an abundance of grassland compared with landscapes with significant amounts of wheat and regional crops (Figure 4.6). A similar pattern was found for the most abundant species of larval overwintering ground beetle, *C. sodalis* (*P* = 0.01, $r^2$ = 0.23) (Figure 4.6).

### *Predatory and herbivorous species*

The activity density of predatory ground beetle species was best predicted by the PC2 model at all spatial scales; the PC2 model at a radius of 1 km had the lowest overall AICc value. Competing models included PC1+D, D, PC2+D and the intercept only model (Table 4.9). The activity density of predatory species was significantly negatively correlated with PC2 (P = 0.04, $r^2$ = 0.17), indicating that their activity density was greater in soybean fields in landscapes with an abundance of regional crops and wheat compared with grassland dominated landscapes (Figure 4.6). Herbivores were best predicted by the intercept model at all spatial scales, competing models included PC1 and PC2.

### *Araneae and landscape variables*

For overall spider activity density, the PC1 + PC2 model had the lowest AIC value at all 6 scales examined. The PC1 + PC2 model at a radius of 1.5 km had the lowest AIC value across scales. Competing models included PC1, PC1 + D, and PC2 + D (Table 4.10). Spider activity density increased with both PC1 and PC2. This relationship was significant for PC1, indicating increased activity density in soybean fields in landscapes surrounded by an abundance of forested habitat ($P = 0.01$, model $r^2=0.35$) (Figure 4.7).

When the two most abundant families of spiders, Lycosidae and Linyphiidae were examined, Linyphiidae had a stronger correlation with landscape variables. The activity density of Lycosidae was best predicted the PC2 model which had the lowest AICc value at all spatial scales; the PC2 model at a radius of 3 km had the lowest AICc value overall (Table 4.11). There was a positive, non-significant correlation between PC1 and the activity density of Lycosidae ($P = 0.06$, $r^2=0.14$) (Figure 4.7). Competing models included PC2 + D, PC1 + PC2, PC1, D, PC2, and the intercept only model. For Linyphiidae activity density, the PC1 model had the lowest AICc value at all spatial scales, the PC1 model at a radius of 3.5 km had the lowest AICc value overall. No competing models were found for Linyphiidae (Table 4.12). There was a significant positive correlation between the Linyphiidae and PC1 ($P = 0.0002$, $r^2=0.44$), indicating greater activity density in soybean fields surrounded by landscapes with an abundance of forested habitat compared with landscapes dominated by corn and soybean fields (Figure 4.7).

## Discussion

A diverse community of Carabidae and Araneae were detected in soybean fields across Iowa, Michigan, Minnesota and Wisconsin, with 62 species of Carabidae and 8 families of Araneae (9 species of Lycosidae) collected in pitfall traps from 26 sites in 2005 and 2006. I examined three hypotheses related to the response of these ground-dwelling arthropods to the surrounding landscape. My first hypothesis was that the activity density of Carabidae, Araneae and Opiliones in soybean would increase with the proportion of semi-natural habitats in the landscape. Rather than a general increase, I found variation in the response of these taxa to landscape composition. The activity density of Araneae supported our hypothesis, increasing in soybean fields in landscapes with an abundance of forests and grasslands. When Carabidae activity density was examined I found that the relationship to landscape varied, with adult overwintering and predatory species increasing and larval overwintering species declining with the abundance of grassland in the landscape. Opiliones activity density was not related to the structure of the surrounding landscape at any of the spatial scales examined.

### *Relationships between Carabidae phenology, trophic level, and landscape composition*

Our data did not support our second hypothesis that predatory Carabidae species that overwinter as adults would be positively correlated with the abundance of semi-natural habitat in the landscape. Instead, predatory species and those that overwinter as adults had greater activity density in soybean fields in agriculturally dominated landscapes. Carabids that overwintered as larvae had greater activity density in soybean fields in landscapes with an abundance of grassland patches. Schmidt et al. (2008) state that although many studies illustrate an increase in the abundance of habitat generalists with the proportion of semi-natural habitat in the landscape, the metapopulations dynamics of habitat generalists are often complex. The response of a particular species to a different habitats in the surrounding landscape may be positive or negative depending on its success in the focal habitat of study. Schmidt et al. (2008) postulate that species well adapted to the focal habitat, in this case a soybean field, will respond negatively to different habitats in the surrounding landscape. Alternatively, species that are better adapted to habitats other than the focal habitat will increase with the amount of this different habitat in the landscape matrix.

This suggests that Carabidae, particularly predators that overwinter as adults are more successful in agricultural systems. Although the majority of the abundant species collected are considered habitat generalists, the most abundant predatory, adult overwintering species found, *P. chalcites*, is thought of as an agricultural specialist (Larsen et al. 2003) and thus is likely to favor agriculturally dominated landscapes. The most abundant species of larval overwintering carabid *C. sodalis* is known to be well adapted to perennial-dominated habitats including grasslands (Larsen et al. 2003). Thus, it follows that this species increases in abundance with the presence of grassland patches in the landscape. Overwintering as an adult gives an advantage of high mobility in search of overwintering sites. These species would be able to disperse from agricultural fields in the fall when conditions deteriorate and recolonize small patches of semi-natural habitat for overwintering whereas less mobile larvae would be less likely to successfully locate them.

I found no evidence of a relationship between landscape composition and the activity density of herbivorous carabids. Overall, herbivores constituted a low percentage of total individuals (8%), the vast majority (94% of herbivores) of which were a single species *H. pensilvanicus.* Other studies have found greater herbivore diversity and seed predation in croplands surrounded by diverse landscapes (Purtauf et al, Menalled et al. 2000). For example, Purtauf et al. (2005) found that the diversity of herbivores in wheat fields in central Germany increased with the proportion of non-crop habitat.

*Araneae and landscape composition*

Araneae had greater activity density in soybean fields in landscapes with an abundance of grassland and forested patches. Semi-natural habitat patches also influenced the activity density of the two most numerous Araneae families collected; Lycosidae and Linyphiidae. The activity density of Lycosidae exhibited a weak, positive correlation with PC2, indicating the abundance of lycosids was greater in soybean fields in landscapes with an abundance of grassland patches. Linyphiidae activity density responded strongly to PC1, increasing in soybean fields in landscapes with an abudance of forested patches. Forested habitat was also an important variable in explaining spider species richness and species composition in oilseed rape fields (Drapela et al. 2007). Overall landscape heterogeneity has also been correlated with spider richness and abundance in wheat fields (Schmidt and Tscharntke 2005, Schmidt et al. 2005, Clough et al. 2005). A stronger response to landscape by Linyphiidae compared with Lycosidae has been documented in other systems. Öberg et al. (2007) found that the activity density of Lycosidae in cereal fields was not related to landscape variables whereas the activity density of Linyphiidae was positively correlated to perennial crops in the surrounding landscape.

*Spatial scale and the dispersal of habitat generalists*

My final hypothesis was that the spatial scale at which an organism responds to landscape would be a function of its capacity for dispersal, thus those that disperse mainly by walking would respond to a smaller spatial scale compared with groups known to frequently utilize flight or ballooning. Carabidae and adult Lycosidae frequently colonized croplands on the ground (Drapela et al. 2007) thus I expected that these groups would respond to a smaller landscape scale compared with the Liniphiidae which frequently balloon throughout their life cycle (Bell et al. 2005). I found support for this hypothesis with walking dispersers responding at smaller spatial scales compared with ballooning species.

The negative response in activity density of all Carabidae, adult-overwintering Carabidae, and predatory Carabidae to grassland abundance was strongest at spatial radi of 1-1.5 km. Carabidae overwintering as larvae and *C. sodalis* responded positively to grassland abundance at a larger spatial scale of 2.5 km. Among spider variables, the response of Lycosidae to the abundance of forested habitats was maximized at 3 km, however AICc values of the best candidate model at each scale were very similar. The response of Linyphiidae increased with spatial scale. Since the positive correlation between Linyphiidae and PC1 was strongest at 3.5 km, our largest spatial scale measured it is possible that these species respond at even larger landscape scales.

*Implications*

How arthropods respond to landscape composition is a function of habitat use and dispersal ability. The distribution and abundance of semi-natural and agricultural habitats within the landscape is likely to greatly influence landscape-scale metapopulation dynamics of habitat generalists. Agriculturally-important organisms often follow a bidirectional movement (Gavish-Regev et al. 2008), moving into agricultural fields when prey populations emerge and back into semi-natural areas in the fall when crops are harvested. Carabidae and Araneae known to routinely cross boundaries from semi-natural habitat patches into agricultural crops (French et al. 2001) but why they do so is vastly understudied. It is likely that some species exhibit bidirectional movement, moving into soybean from semi-natural habitats in response to prey availability. Alternatively, species may be exhibiting negligible movement (Gavish-Regev et al. 2008) through agricultural habitats, where individuals move through an unsuitable habitat to colonize other patches of suitable habitat (Gavish-Regev et al. 2008). A reduction in semi-natural habitat may force species to disperse through soybean to colonize isolated patches of preferred habitat. Understanding how habitat generalists that vary in their capacity for dispersal utilize agricultural habitats has implications for biological control as well as the conservation of biodiversity. Well established patterns exist that illustrate the influence of landscape structure on these organisms in several agricultural systems, it is time to begin building an understanding of the functioning of these organisms at the metacommunity level.

Table 4.1. Land cover categories used in the calculation of Simpson's Diversity Index (D) and as variables included in the principal components analysis.

| Simpson's Diversity (D) | PCA |
|---|---|
| Cropland Categories | |
| Corn | Corn |
| Soybean | Soybean |
| Wheat | |
| Sugar Beet | Other Crops[1] |
| Orchard | |
| Dry Bean | |
| Sunflower | |
| Cabbage | |
| Canola | |
| Potato | |
| Carrot | |
| Squash | |
| Ornamental Crops | |
| Tilled Field | |
| Non-Crop Categories | |
| Forage | Grassland[2] |
| Old Field and Restored Prairie | |
| Pastureland | |
| Forested | Forest |
| Wetlands and Open Water | Water |
| Urban | Urban |

[1] Other Crops contains all Simpson's D cropland categories except corn, soybean, and wheat.

[2] Grassland contains the Simpson's D non-crop categories Forage, Old Field and Restored Prairie, and Pastureland

Table 4.2. Models compared by AICc analysis at spatial radii of 1-3.5 km.

$\mathrm{y} = B_o$

$\mathrm{y} = B_o + B_1\mathrm{PC1}$

$\mathrm{y} = B_o + B_1\mathrm{PC2}$

$\mathrm{y} = B_o + B_1\mathrm{D}$

$\mathrm{y} = B_o + B_1\mathrm{PC1} + B_2\mathrm{PC2}$

$\mathrm{y} = B_o + B_1\mathrm{PC1} + B_2\mathrm{D}$

$\mathrm{y} = B_o + B_1\mathrm{PC2} + B_2\mathrm{D}$

$\mathrm{y} = B_o + B_1\mathrm{PC1} + B_2\mathrm{PC2} + B_3\mathrm{D}$

Table 4.3. Abundance, trophic level and overwintering stage of Carabidae species found in soybean fields in Iowa, Michigan, Minnesota, and Wisconsin.

| Species | N | Feeding[1] | Overwintering[2] |
|---|---|---|---|
| *Agonum cupreum* | 3 | P | A |
| *Agonum cupripenne* | 21 | P | A |
| *Agonum octopunctatum* | 2 | P | A |
| *Agonum placidum* | 224 | P | A |
| *Amara aenea* | 93 | H | A |
| *Amara impunctata* | 1 | H | A |
| *Amara obesa* | 3 | H | A |
| *Amara spp.* | 1 | X | X |
| *Anisodactylus harrissii* | 4 | P | A |
| *Anisodactylus rusticus* | 15 | P | A |
| *Anisodactylus sanctaecrucis* | 74 | P | A |
| *Bembidion femoratum* | 23 | P | A |
| *Bembidion nitidum* | 27 | P | A |
| *Bembidion obtusum* | 1 | P | A |
| *Bembidion quadrimaculatum* | 85 | P | A |
| *Bembidion rapidum* | 36 | P | A |
| *Bembidion rupicola* | 4 | P | A |
| *Brachinus ovipennis* | 62 | P | A |
| *Calathus gregarius* | 5 | O | A |
| *Calosoma calidum* | 1 | P | A |
| *Chlaenius sericeus* | 2 | P | A |
| *Chlaenius platyderus* | 1 | P | A |
| *Chlaenius pusillus* | 86 | P | A |
| *Chlaenius tomentosus* | 1 | P | A |
| *Chlaenius tricolor* | 152 | P | A |
| *Clivina bipustulata* | 59 | P | L |
| *Clivina impressefrons* | 31 | P | A |
| *Clivina spp.* | 2 | X | X |
| *Cyclotrachelus seximpressus* | 5 | P | L |
| *Cyclotrachelus sodalis* | 11121 | P | L |
| *Dicaelus elongatus* | 43 | P | A |
| *Dyschirius globulosus* | 1 | P | A |
| *Elaphropus anceps* | 61 | P | A |
| *Galerita janus* | 4 | P | A |
| *Geopinus incrassatus* | 140 | P | A |

Table 4.3 (continued)

| Species (continued) | N | Feeding[1] | Overwintering[2] |
|---|---|---|---|
| *Harpalus affinis* | 36 | P | A |
| *Harpalus caliginosus* | 44 | P | A |
| *Harpalus erraticus* | 1310 | P | A |
| *Harpalus herbaivagus* | 42 | H | A |
| *Harpalus pensylvanicus* | 2267 | H | L |
| *Lebia fuscata* | 1 | P | A |
| *Lebia spp.* | 2 | X | X |
| *Leptotrachelus dorsalis* | 1 | X | X |
| *Poecilus chalcites* | 7806 | P | A |
| *Poecilus lucublandus* | 1254 | P | A |
| *Pterostichus commutabilis* | 14 | X | A |
| *Pterostichus femoralis* | 6 | X | X |
| *Pterostichus melanarius* | 688 | P | L |
| *Pterostichus permundus* | 2380 | P | L |
| *Scarites quadriceps* | 847 | P | A |
| *Stenolophus comma* | 145 | P | A |
| *Stenolophus lecontei* | 1 | P | A |
| *Stenolophus ochropezus* | 5 | P | A |
| *Stroluphus chropezus* | 1 | P | A |
| *Synuchus impunctatus* | 3 | P | A |
| *Trechus quadristriatus* | 27 | P | L |
| unknown species 1 | 2 | X | X |
| unknown species 2 | 3 | X | X |
| unknown species 3 | 1 | X | X |
| unknown species 4 | 1 | X | X |
| unknown species 5 | 1 | X | X |
| Carabidae | 29300 | | |

[1] Carabidae are classified by trophic level as either H for herbivorous, P for predatory or omnivorous, or X for unknown.

[2] Carabidae are classified by overwintering stage as either A for adult, H for larva, or X for unknown.

Table 4.4. Carabidae community composition in soybean fields in Iowa, Michigan, Minnesota and Wisconsin in 2005-2006.

| Species | Iowa | Michigan | Wisconsin | Minnesota |
|---|---|---|---|---|
| *Acupalpus partiarius* | 0 | 0 | 0 | 0 |
| *Agonum cupreum* | 0 | 0.03 | 0.04 | 0 |
| *Agonum cupripenne* | 0.01 | 0.25 | 0.07 | 0 |
| *Agonum octopunctatum* | 0 | 0.03 | 0 | 0 |
| *Agonum placidum* | 0.07 | 1.49 | 1.56 | 1.55 |
| *Amara aenea* | 0 | 1.23 | 0.07 | 0.05 |
| *Amara impunctata* | 0 | 0.01 | 0 | 0 |
| *Amara obesa* | 0.02 | 0 | 0 | 0 |
| *Amara spp.* | 0.01 | 0 | 0 | 0 |
| *Anisodactylus harrissii* | 0.03 | 0 | 0 | 0 |
| *Anisodactylus rusticus* | 0.02 | 0.08 | 0.11 | 0.08 |
| *Anisodactylus sanctaecrucis* | 0.03 | 0.76 | 0.46 | 0.05 |
| *Bembidion femoratum* | 0 | 0.04 | 0.64 | 0.05 |
| *Bembidion nitidum* | 0 | 0.33 | 0.11 | 0 |
| *Bembidion obtusum* | 0 | 0.01 | 0.00 | 0 |
| *Bembidion quadrimaculatum* | 0 | 0.19 | 1.84 | 0.48 |
| *Bembidion rapidum* | 0.16 | 0.15 | 0 | 0 |
| *Bembidion rupicola* | 0 | 0.06 | 0 | 0 |
| *Brachinus ovipennis* | 0 | 0.35 | 0 | 0.93 |
| *Calathus gregarius* | 0.03 | 0.01 | 0 | 0 |
| *Calosoma calidum* | 0 | 0 | 0.04 | 0 |
| *Chlaenius sericeus* | 0 | 0 | 0 | 0.05 |
| *Chlaenius platyderus* | 0.01 | 0 | 0 | 0 |
| *Chlaenius pusillus* | 0.51 | 0.10 | 0 | 0.03 |
| *Chlaenius tomentosus* | 0.01 | 0.00 | 0 | 0 |
| *Chlaenius tricolor* | 0.77 | 0.36 | 0.32 | 0 |
| *Clivina bibustulata* | 0.29 | 0.21 | 0 | 0 |
| *Clivina impressefrons* | 0.03 | 0.36 | 0 | 0 |
| *Clivina spp.* | 0.01 | 0 | 0.04 | 0 |
| *Cyclotrachelus seximpressus* | 0.03 | 0 | 0 | 0 |
| *Cyclotrachelus sodalis* | 51.10 | 11.88 | 4.25 | 58.80 |
| *Dicaelus elongatus* | 0.28 | 0 | 0 | 0 |
| *Dyschirius globulosus* | 0 | 0 | 0 | 0.03 |

Table 4.4 (continued)

| Species (continued) | Iowa | Michigan | Wisconsin | Minnesota |
|---|---|---|---|---|
| *Elaphropus anceps* | 0.20 | 0.28 | 0.39 | 0 |
| *Galerita janus* | 0.03 | 0 | 0 | 0 |
| *Geopinus incrassatus* | 0 | 0 | 4.96 | 0 |
| *Harpalus affinis* | 0 | 0.43 | 0.07 | 0.08 |
| *Harpalus caliginosus* | 0.28 | 0 | 0.04 | 0.03 |
| *Harpalus erraticus* | 0.01 | 0.01 | 46.37 | 0 |
| *Harpalus herbaivagus* | 0.05 | 0.17 | 0.35 | 3.64 |
| *Harpalus pensylvanicus* | 2.94 | 8.90 | 12.12 | 20.89 |
| *Lebia fuscata* | 0 | 0.01 | 0 | 0 |
| *Lebia spp.* | 0.01 | 0 | 0 | 0 |
| *Leptotrachelus dorsalis* | 0.01 | 0 | 0 | 0 |
| *Poecilus chalcites* | 18.91 | 61.39 | 4.47 | 8.88 |
| *Poecilus lucublandus* | 5.90 | 0.72 | 1.31 | 6.62 |
| *Pterostichus commutabilis* | 0.01 | 0.08 | 0.25 | 0 |
| *Pterostichus femoralis* | 0.04 | 0 | 0 | 0 |
| *Pterostichus melanarius* | 0.07 | 2.96 | 16.27 | 0.10 |
| *Pterostichus permundus* | 13.13 | 4.67 | 0.25 | 0.80 |
| *Scarites quadriceps* | 4.88 | 0.98 | 0.82 | 0.23 |
| *Stenolophus comma* | 0.04 | 0.97 | 2.45 | 0 |
| *Stenolophus lecontei* | 0.01 | 0 | 0 | 0 |
| *Stenolophus ochropezus* | 0.03 | 0 | 0 | 0 |
| *Stroluphus chropezus* | 0.01 | 0 | 0 | 0 |
| *Synuchus impunctatus* | 0 | 0.01 | 0.07 | 0 |
| *Trechus quadristriatus* | 0.00 | 0.37 | 0.00 | 0 |
| unknown 1 | 0 | 0.01 | 0.07 | 0 |
| unknown 2 | 0 | 0 | 0.04 | 0 |
| unknown 3 | 0 | 0 | 0.04 | 0 |
| unknown 4 | 0.01 | 0 | 0 | 0 |
| unknown 5 | 0.01 | 0 | 0 | 0 |

Table 4.5. Spider community composition in soybean fields in Iowa, Michigan, Minnesota and Wisconsin in 2005-2006. All spiders were identified to family, Lycosidae were identified to genus and where possible, species.

| | Percentage of Total Araneae | | | |
|---|---|---|---|---|
| Family | IA | MI | MN | WI |
| Agelinidae | 0.25 | 0.23 | 2.42 | 2.81 |
| Araneidae | 0 | 0.15 | 0 | 0 |
| Gnaphosidae | 0.98 | 0.30 | 1.61 | 0.56 |
| Linyphiidae | 2.66 | 28.33 | 53.23 | 34.27 |
| Lycosidae | 88.77 | 66.31 | 40.32 | 61.42 |
| Oxyopidae | 0.25 | 0 | 0 | 0 |
| Salticidae | 0.45 | 1.66 | 0 | 0.37 |
| Tetragnathidae | 0 | 0.23 | 0 | 0 |
| Thomisidae | 6.66 | 2.79 | 2.42 | 0.56 |

| | Percentage of Total Lycosidae | | | |
|---|---|---|---|---|
| Lycosidae Species | IA | MI | MN | WI |
| *Allocosa modesta* | 0.18 | 0.34 | 0 | 0 |
| *Hogna helluo* | 4.37 | 1.36 | 0 | 1.22 |
| *Pardosa saxatilis* | 26.55 | 34.09 | 0 | 21.65 |
| *Pardosa* sp. 1 | 0 | 2.61 | 0 | 0 |
| *Pardosa* sp. 2 | 0 | 0 | 0 | 3.05 |
| *Schizocosa avaida* | 6.53 | 3.64 | 80.00 | 3.96 |
| *Schzocosa crassipes* | 27.06 | 0.23 | 0 | 4.57 |
| *Trochosa terricola* | 0.97 | 25.00 | 8.00 | 35.98 |
| *Varacosa avara* | 0.64 | 0.11 | 2.00 | 0 |
| Immature | 31.75 | 30.45 | 10.00 | 29.27 |
| Damaged | 1.94 | 2.16 | 0 | 0.30 |

Table 4.6. Summary of model selection statistics for evaluating the activity density of Carabidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1] [2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| **1.0 km** | $\boldsymbol{B_0 + B_1(PC2)^{\dagger}}$ | **-27.83** | **3** | **62.74** | **0.00** | **0.39** | **0.13** | |
| 1.0 km | $B_0$ | -30.10 | 2 | 64.72 | 1.98 | 0.15 | | |
| 1.0 km | $B_0 + B_1(PC1) + B_2(PC2)^{\dagger}$ | -27.49 | 4 | 64.90 | 2.16 | 0.13 | 0.11 | PC1= -0.16, PC2= -0.40 |
| 1.5 km | $B_0 + B_1(PC2)$ | -28.05 | 3 | 63.18 | 0.00 | 0.36 | 0.11 | |
| 1.5 km | $B_0$ | -30.10 | 2 | 64.72 | 1.54 | 0.17 | | |
| 2.0 km | $B_0 + B_1(PC2)$ | -28.25 | 3 | 63.58 | 0.00 | 0.33 | 0.1 | |
| 2.0 km | $B_0$ | -30.10 | 2 | 64.72 | 1.14 | 0.19 | | |
| 2.5 km | $B_0 + B_1(PC2)$ | -28.77 | 3 | 64.62 | 0.00 | 0.30 | 0.1 | |
| 2.5 km | $B_0$ | -30.10 | 2 | 64.72 | 0.10 | 0.28 | | |
| 3.0 km | $B_0 + B_1(PC2)$ | -28.66 | 3 | 64.40 | 0.00 | 0.28 | 0.07 | |
| 3.0 km | $B_0$ | -30.10 | 2 | 64.72 | 0.32 | 0.24 | | |
| 3.5 km | $B_0 + B_1(PC2)$ | -28.70 | 3 | 64.48 | 0.00 | 0.31 | 0.07 | |
| 3.5 km | $B_0$ | -30.10 | 2 | 64.72 | 0.24 | 0.27 | | |

[1] $^{\dagger}$Indicates a variable was significant at $P < 0.05$

[2] Variables in parentheses indicate a negative relationship with Carabidae activity density

Table 4.7. Summary of model selection statistics for evaluating the activity density of adult-overwintering Carabidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model$^{1\ 2\ 3}$ | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| **1.0 km** | $\boldsymbol{B_0 + B_1(\mathrm{PC2})^{\dagger\dagger\dagger}}$ | **-23.08** | **3** | **53.24** | **0.00** | **0.47** | **0.55** | |
| 1.0 km | $B_0 + B_1(\mathrm{PC1}) + B_2(\mathrm{PC2})^{\dagger\dagger} + \mathrm{D}$ | -20.89 | 5 | 54.78 | 1.54 | 0.22 | 0.59 | PC1= -0.39, PC2= -0.59, D= 0.34 |
| 1.0 km | $B_0 + B_1(\mathrm{PC1}) + B_2(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -22.49 | 4 | 54.90 | 1.66 | 0.20 | 0.55 | PC1= -0.21, PC2= -0.76 |
| 1.5 km | $B_0 + B_1(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -23.15 | 3 | 53.38 | 0.00 | 0.42 | 0.55 | |
| 1.5 km | $B_0 + B_1(\mathrm{PC1}) + B_2(\mathrm{PC2})^{\dagger\dagger} + \mathrm{D}^{\dagger}$ | -20.56 | 5 | 54.12 | 0.74 | 0.29 | 0.6 | PC1= -0.37, PC2= -0.63, D=0.42 |
| 1.5 km | $B_0 + B_1\mathrm{D} + B_2(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -22.51 | 4 | 54.94 | 1.56 | 0.19 | 0.55 | D=0.23, PC2= -0.72 |
| 2.0 km | $B_0 + B_1(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -24.24 | 3 | 55.56 | 0.00 | 0.46 | 0.51 | |
| 2.0 km | $B_0 + B_1(\mathrm{PC1}) + B_2(\mathrm{PC2})^{\dagger\dagger\dagger} + \mathrm{D}^{\dagger}$ | -21.34 | 5 | 55.68 | 0.12 | 0.43 | 0.57 | PC1= -0.37, PC2= -0.69, D=0.45 |
| 2.0 km | $B_0 + B_1\mathrm{D} + B_2(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -23.26 | 4 | 56.44 | 0.88 | 0.29 | 0.53 | PC2= -0.71, D=0.27 |
| 2.5 km | $B_0 + B_1(\mathrm{PC1}) + B_2(\mathrm{PC2})^{\dagger\dagger\dagger} + \mathrm{D}^{\dagger}$ | -23.01 | 5 | 59.02 | 0.00 | 0.40 | 0.51 | PC1= -0.40, PC2= -0.64, D=0.46 |
| 2.5 km | $B_0 + B_1(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -26.20 | 3 | 59.48 | 0.46 | 0.32 | 0.43 | |
| 2.5 km | $B_0 + B_1\mathrm{D} + B_2(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -25.27 | 4 | 60.46 | 1.44 | 0.20 | 0.45 | PC2= -0.66, D=0.26 |

Table 4.7 (continued)

| Radius (km) | Model$^{1\ 2\ 3}$ | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 3.0 km | $B_0 + B_1(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -26.53 | 3 | 60.14 | 0.00 | 0.34 | 0.42 | |
| 3.0 km | $B_0 + B_1(\mathrm{PC1}) + B_2(\mathrm{PC2})^{\dagger\dagger\dagger} + \mathrm{D}^{\dagger}$ | -23.77 | 5 | 60.54 | 0.40 | 0.28 | 0.49 | PC1= -0.34, PC2= -0.65, D=0.44 |
| 3.0 km | $B_0 + B_1\mathrm{D}^{\dagger} + B_2(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -25.42 | 4 | 60.76 | 0.62 | 0.25 | 0.44 | PC2= -0.66, D=0.29 |
| 3.5 km | $B_0 + B_1(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -26.76 | 3 | 60.60 | 0.00 | 0.49 | 0.41 | |
| 3.5 km | $B_0 + B_1\mathrm{D} + B_2(\mathrm{PC2})^{\dagger\dagger\dagger}$ | -25.98 | 4 | 61.88 | 1.28 | 0.26 | 0.42 | PC2= -0.65, D=0.24 |

[1] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] †Indicates a variable was significant at $P < 0.05$, †† indicates $P < 0.01$, ††† indicates $P < 0.001$

[3] Variables in parentheses indicate a negative relationship with activity density

Table 4.8. Summary of model selection statistics for evaluating the activity density of larval-overwintering Carabidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model$^{1\ 2}$ | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 1.0 km | $B_0 + B_1\mathrm{PC2}^{\dagger}$ | -33.44 | 3 | 73.96 | 0.00 | 0.34 | 0.17 | |
| 1.0 km | $B_0 + B_1(\mathrm{D}) + B_2\mathrm{PC2}$ | -32.69 | 4 | 75.30 | 1.34 | 0.17 | 0.18 | PC2=0.35, D= -0.24 |
| 1.0 km | $B_0 + B_1(\mathrm{D})$ | -34.44 | 3 | 75.96 | 2.00 | 0.12 | 0.1 | |
| 1.5 km | $B_0 + B_1\mathrm{PC2}^{\dagger}$ | -33.20 | 3 | 73.48 | 0.00 | 0.32 | 0.18 | |
| 1.5 km | $B_0 + B_1(\mathrm{D}) + B_2\mathrm{PC2}$ | -32.16 | 4 | 74.24 | 0.76 | 0.22 | 0.21 | PC2=0.39, D= -0.28 |
| 1.5 km | $B_0 + B_1(\mathrm{PC1}) + B_2\mathrm{PC2}^{\dagger}$ | -32.36 | 4 | 74.64 | 1.16 | 0.18 | 0.2 | PC1= -0.25, PC2=0.48 |
| **2.0 km** | $\boldsymbol{B_0 + B_1\mathrm{PC2}^{\dagger}}$ | **-33.21** | **3** | **73.50** | **0.00** | **0.40** | **0.18** | |
| 2.0 km | $B_0 + B_1(\mathrm{PC1}) + B_2\mathrm{PC2}^{\dagger}$ | -32.44 | 4 | 74.80 | 1.30 | 0.21 | 0.2 | PC1= -0.24, PC2=0.47 |
| 2.0 km | $B_0 + B_1(\mathrm{D}) + B_2\mathrm{PC2}^{\dagger}$ | -32.58 | 4 | 75.08 | 1.58 | 0.18 | 0.19 | PC2=0.43, D= -0.22 |
| 2.5 km | $B_0 + B_1\mathrm{PC2}^{\dagger}$ | -32.89 | 3 | 72.86 | 0.00 | 0.45 | 0.2 | |
| 2.5 km | $B_0 + B_1(\mathrm{D}) + B_2\mathrm{PC2}^{\dagger}$ | -32.30 | 4 | 74.52 | 1.66 | 0.20 | 0.2 | PC2=0.45, D= -0.21 |
| 2.5 km | $B_0 + B_1(\mathrm{PC1}) + B_2\mathrm{PC2}^{\dagger}$ | -32.34 | 4 | 74.60 | 1.74 | 0.19 | 0.2 | PC1= -0.20, PC2=0.49 |

Table 4.8 (continued)

| Radius (km) | Model[1] [2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 3.0 km | $B_0 + B_1\mathrm{PC2}^\dagger$ | -33.42 | 3 | 73.92 | 0.00 | 0.46 | 0.17 | |
| 3.0 km | $B_0 + B_1(\mathrm{PC1}) + B_2\mathrm{PC2}^\dagger$ | -32.98 | 4 | 75.88 | 1.96 | 0.17 | 0.16 | PC1= -0.18, PC2=0.46 |
| 3.5 km | $B_0 + B_1\mathrm{PC2}^\dagger$ | -33.61 | 3 | 74.30 | 0.00 | 0.46 | 0.16 | |

[1] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] †Indicates a variable was significant at $P < 0.05$

[3] Variables in parentheses indicate a negative relationship with activity density

Table 4.9. Summary of model selection statistics for evaluating the activity density of predatory Carabidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1] [2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| **1.0 km** | $\boldsymbol{B_0 + B_1(PC2)^{\dagger}}$ | **-31.97** | **3** | **71.02** | **0.00** | **0.43** | **0.13** | |
| 1.5 km | $B_0 + B_1(PC2)^{\dagger}$ | -32.03 | 3 | 71.14 | 0.00 | 0.42 | 0.13 | |
| 2.0 km | $B_0 + B_1(PC2)$ | -32.53 | 3 | 72.14 | 0.00 | 0.35 | 0.1 | |
| 2.0 km | $B_0$ | -34.38 | 2 | 73.28 | 1.14 | 0.20 | | |
| 2.5 km | $B_0 + B_1(PC2)$ | -32.95 | 3 | 72.98 | 0.00 | 0.27 | 0.06 | |
| 2.5 km | $B_0$ | -34.38 | 2 | 73.28 | 0.30 | 0.24 | | |
| 2.5 km | $B_0 + B_1D + B_2(PC1)$ | -32.43 | 4 | 74.78 | 1.80 | 0.11 | 0.06 | PC2= -0.30, D=0.13 |
| 2.5 km | $B_0 + B_1D$ | -33.95 | 3 | 74.98 | 2.00 | 0.10 | -0.01 | |
| 3.0 km | $B_0 + B_1(PC2)$ | -32.67 | 3 | 72.42 | 0.00 | 0.30 | 0.09 | |
| 3.0 km | $B_0$ | -34.38 | 2 | 73.28 | 0.86 | 0.20 | | |
| 3.0 km | $B_0 + B_1D + B_2(PC2)$ | -32.23 | 4 | 74.38 | 1.96 | 0.11 | 0.08 | PC2= -0.32, D=0.18 |
| 3.5 km | $B_0 + B_1(PC2)$ | -32.64 | 3 | 72.36 | 0.00 | 0.33 | 0.09 | |
| 3.5 km | $B_0$ | -34.38 | 2 | 73.28 | 0.92 | 0.21 | | |

[1] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] $^{\dagger}$Indicates a variable was significant at $P < 0.05$

[3] Variables in parentheses indicate a negative relationship with activity density

Table 4.10. Summary of model selection statistics for evaluating the activity density of Araneae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model$^{1\ 2}$ | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 1 km | $B_0 + B_1\mathrm{PC1}^{\dagger} + B_2\mathrm{PC2}$ | -17.35 | 4 | 44.62 | 0.00 | 0.04 | 0.23 | PC1=0.47, PC2=0.33 |
| 1 km | $B_0 + B_1\mathrm{PC1}^{\dagger}$ | -18.81 | 3 | 44.70 | 0.08 | 0.04 | 0.17 | |
| 1 km | $B_0 + B_1(\mathrm{D}) + B_2\mathrm{PC1}^{\dagger}$ | -18.23 | 4 | 46.38 | 1.76 | 0.02 | 0.17 | PC1=0.43, D= -0.21 |
| 1 km | $B_0 + B_1(\mathrm{D})^{\dagger} + B_2\mathrm{PC2}^{\dagger}$ | -18.23 | 4 | 46.38 | 1.76 | 0.02 | 0.17 | D=0.41, PC2=0.43 |
| **1.5 km** | **$B_0 + B_1\mathrm{PC1}^{\dagger\dagger} + B_2\mathrm{PC2}$** | **-16.19** | **4** | **42.30** | **0.00** | **0.42** | **0.29** | **PC1=0.52, PC2=0.39** |
| 1.5 km | $B_0 + B_1\mathrm{PC1}^{\dagger}$ | -18.3 | 3 | 43.68 | 1.38 | 0.21 | 0.2 | |
| 2.0 km | $B_0 + B_1\mathrm{PC1}^{\dagger\dagger} + B_2\mathrm{PC2}$ | -16.27 | 4 | 42.46 | 0.00 | 0.42 | 0.29 | PC1=0.52, PC2=0.36 |
| 2.0 km | $B_0 + B_1\mathrm{PC1}^{\dagger\dagger}$ | -18.11 | 3 | 43.30 | 0.84 | 0.27 | 0.21 | |
| 2.5 km | $B_0 + B_1\mathrm{PC1}^{\dagger} + B_2\mathrm{PC2}$ | -17.13 | 4 | 44.18 | 0.00 | 0.33 | 0.24 | PC1=0.49, PC2=33 |
| 2.5 km | $B_0 + B_1\mathrm{PC1}^{\dagger}$ | -18.59 | 3 | 44.26 | 0.08 | 0.32 | 0.19 | |

Table 4.10 (continued)

| Radius (km) | Model[1] [2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 3.0 km | $B_0 + B_1\text{PC1}^{\dagger} + B_2\text{PC2}$ | -17.05 | 4 | 44.02 | 0.00 | 0.39 | 0.24 | PC1=0.48, PC2=0.35 |
| 3.0 km | $B_0 + B_1\text{PC1}^{\dagger}$ | -18.79 | 3 | 44.66 | 0.64 | 0.28 | 0.17 | |
| 3.5 km | $B_0 + B_1\text{PC1}^{\dagger} + B_2\text{PC2}$ | -17.1 | 4 | 44.12 | 0.00 | 0.36 | 0.24 | PC1=0.48, PC2=0.34 |
| 3.5 km | $B_0 + B_1\text{PC1}^{\dagger}$ | -18.73 | 3 | 44.54 | 0.42 | 0.29 | 0.18 | |

[1] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] †Indicates a variable was significant at $P < 0.05$

[3] Variables in parentheses indicate a negative relationship with activity density

Table 4.11. Summary of model selection statistics for evaluating the activity density of Lycosidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1 2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 1.0 km | $B_0 + B_1$PC2 | -18.88 | 3 | 44.84 | 0.00 | 0.30 | 0.1 | |
| 1.0 km | $B_0 + B_1$D + $B_2$PC2[†] | -18.04 | 4 | 46.00 | 1.16 | 0.17 | 0.12 | PC2=0.43, D=0.25 |
| 1.0 km | $B_0 + B_1$PC1+ $B_2$PC2 | -18.05 | 4 | 46.02 | 1.18 | 0.17 | 0.12 | PC1=0.25, PC2=0.38 |
| 1.0 km | $B_0$ | -20.82 | 2 | 46.16 | 1.32 | 0.16 | | |
| 1.5 km | $B_0 + B_1$PC2 | -18.89 | 3 | 44.86 | 0.00 | 0.29 | 0.1 | |
| 1.5 km | $B_0 + B_1$PC1+ $B_2$PC2 | -17.86 | 4 | 45.64 | 0.78 | 0.19 | 0.13 | PC1=0.28, PC2=0.38 |
| 1.5 km | $B_0$ | -20.82 | 2 | 46.16 | 1.30 | 0.15 | | |
| 1.5 km | $B_0 + B_1$D + $B_2$PC2[†] | -18.36 | 4 | 46.64 | 1.78 | 0.12 | 0.1 | PC2=0.41, D=0.20 |
| **2.0 km** | **$B_0 + B_1$PC2** | **-19.07** | **3** | **45.22** | **0.46** | **0.27** | **0.1** | |
| 2.0 km | $B_0 + B_1$PC1+ $B_2$PC2 | -17.95 | 4 | 45.82 | 1.06 | 0.20 | 0.13 | PC1=0.29, PC2=0.37 |
| 2.0 km | $B_0$ | -20.82 | 2 | 46.16 | 1.40 | 0.17 | | |
| 2.0 km | $B_0 + B_1$PC1 | -19.84 | 3 | 46.76 | 2.00 | 0.12 | 0.03 | |
| 2.5 km | $B_0 + B_1$PC2 | -19.10 | 3 | 45.28 | 0.00 | 0.29 | 0.09 | |
| 2.5 km | $B_0$ | -20.82 | 2 | 46.16 | 0.88 | 0.19 | | |

Table 4.11 (continued)

| Radius (km) | Model[1] [2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 2.5 km | $B_0 + B_1$PC1+ $B_2$PC2 | -18.26 | 4 | 46.44 | 1.16 | 0.16 | 0.11 | PC1=0.25, PC2=0.36 |
| 2.5 km | $B_0 + B_1$PC1 | -20.01 | 3 | 47.10 | 1.82 | 0.12 | 0.02 | |
| 2.5 km | $B_0 + B_1$D + $B_2$PC2 | -18.60 | 4 | 47.12 | 1.84 | 0.12 | 0.08 | PC2=0.38, D=0.20 |
| 3.0 km | $B_0 + B_1$PC2 | -18.87 | 3 | 44.82 | 0.00 | 0.33 | 0.1 | |
| 3.0 km | $B_0 + B_1$PC1+ $B_2$PC2 | -18.10 | 4 | 46.12 | 1.30 | 0.17 | 0.12 | PC1=0.24, PC2=0.38 |
| 3.0 km | $B_0$ | -20.82 | 2 | 46.16 | 1.34 | 0.17 | | |
| 3.0 km | $B_0 + B_1$D + $B_2$PC2$^\dagger$ | -18.44 | 4 | 46.80 | 1.98 | 0.12 | 0.09 | PC2=0.40, D=0.18 |
| 3.5 km | $B_0 + B_1$PC2 | -18.92 | 3 | 44.92 | 0.00 | 0.31 | 0.1 | |
| 3.5 km | $B_0$ | -20.82 | 2 | 46.16 | 1.24 | 0.17 | | |
| 3.5 km | $B_0 + B_1$PC1+ $B_2$PC2 | -18.13 | 4 | 46.18 | 1.26 | 0.16 | 0.12 | PC1=0.24, PC2=0.38 |
| 3.5 km | $B_0 + B_1$D + $B_2$PC2$^\dagger$ | -18.23 | 4 | 46.38 | 1.46 | 0.15 | 0.1 | PC2=0.40, D=0.23 |

[1] D = Simpson's Diversity where D = $1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] $^\dagger$Indicates a variable was significant at $P < 0.05$

Table 4.12. Summary of model selection statistics for evaluating the activity density of Linyphiidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ |
|---|---|---|---|---|---|---|---|
| 1.0 km | $B_0 + B_1\mathrm{PC1}^{††}$ | -7.18 | 3 | 21.44 | 0.00 | 0.05 | 0.34 |
| 1.5 km | $B_0 + B_1\mathrm{PC1}^{†††}$ | -6.37 | 3 | 19.82 | 0.00 | 0.55 | 0.38 |
| 2.0 km | $B_0 + B_1\mathrm{PC1}^{†††}$ | -6.07 | 3 | 19.22 | 0.00 | 0.59 | 0.39 |
| 2.5 km | $B_0 + B_1\mathrm{PC1}^{†††}$ | -5.95 | 3 | 18.98 | 0.00 | 0.61 | 0.40 |
| 3.0 km | $B_0 + B_1\mathrm{PC1}^{†††}$ | -5.91 | 3 | 18.90 | 0.00 | 0.61 | 0.40 |
| 3.5 km | $B_0 + B_1\mathrm{PC1}^{†††}$ | -5.56 | 3 | 18.20 | 0.00 | 0.60 | 0.42 |

[1] †Indicates a variable was significant at $P < 0.01$, ††† indicates $P < 0.001$

Figure 4.1.

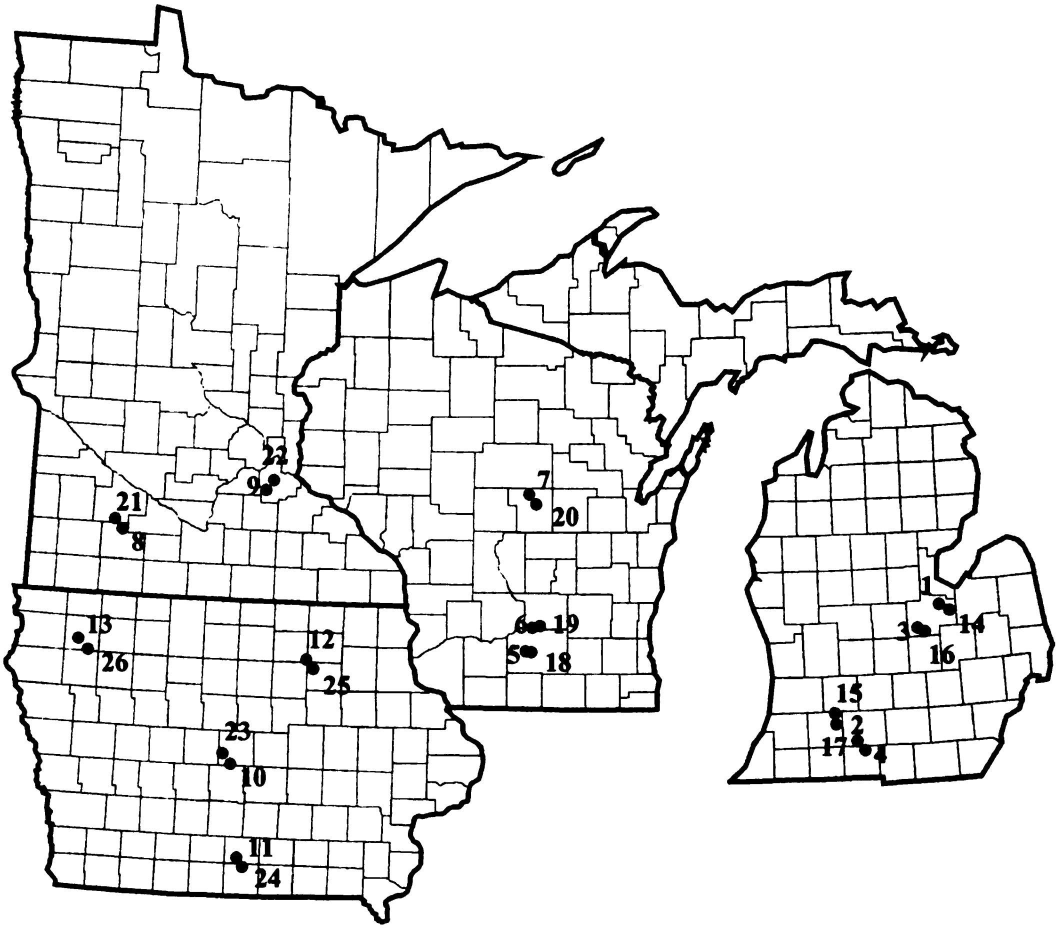


Figure 4.1. Map of soybean study sites sampled for Carabidae, Opiliones and Araneae in 2005 (1-13) and 2006 (14-26) using pitfall traps. Sites were selected so that the 3.5 km landscape radius surrounding each field varied in diversity and the abundance of semi-natural and agricultural habitat.

Figure 4.2.

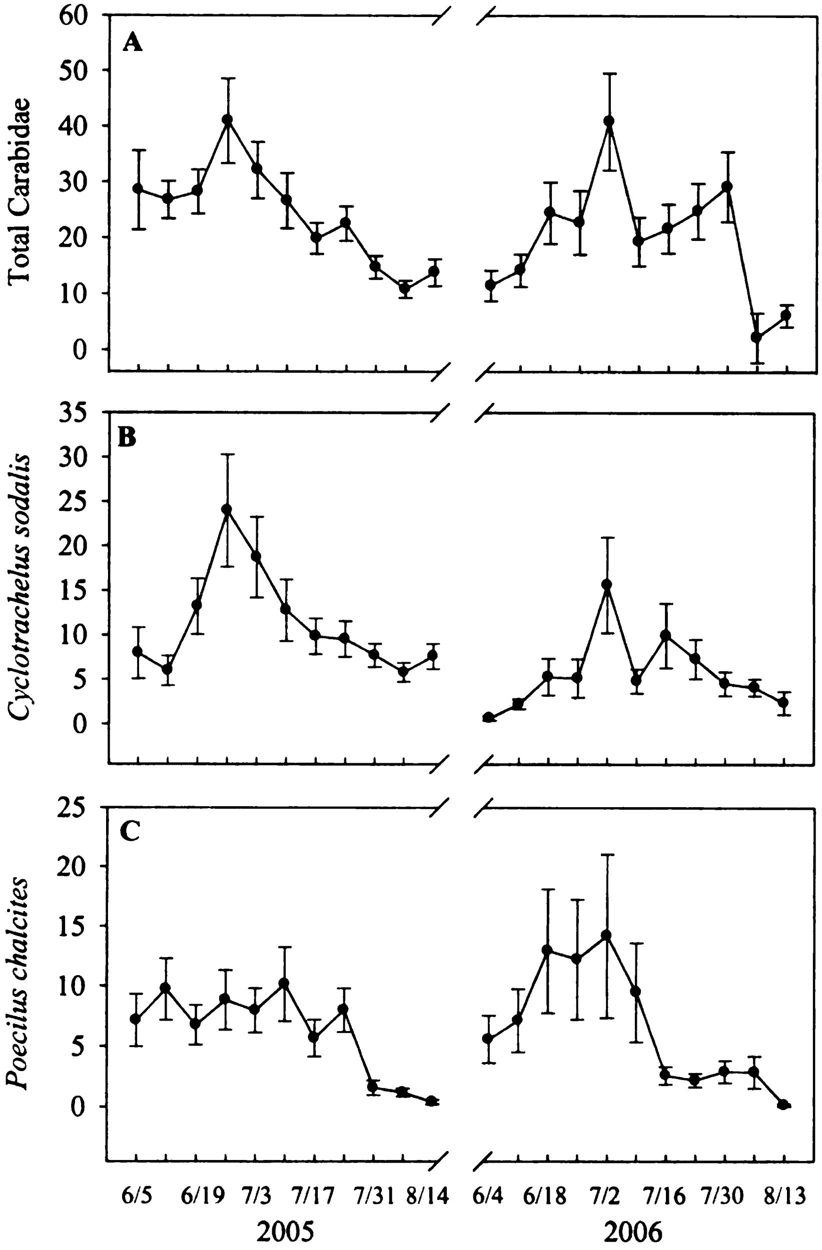


Figure 4.2. Activity density by date of (A) total Carabidae (B) *C. sodalis*, (C) *P. chalcites*, (D) *P. permundus*, (E) *H. pensylvanicus*, (F) *H. erraticus*, (see page 120) G) *P. lucublandus*, (H) *S. quadriceps*, and (I) *P. melanarius* (see page 121) collected per pitfall trap for the 26 soybean fields sampled in 2005 and 2006. Species are shown in order of overall abundance.

Figure 4.2 (continued)

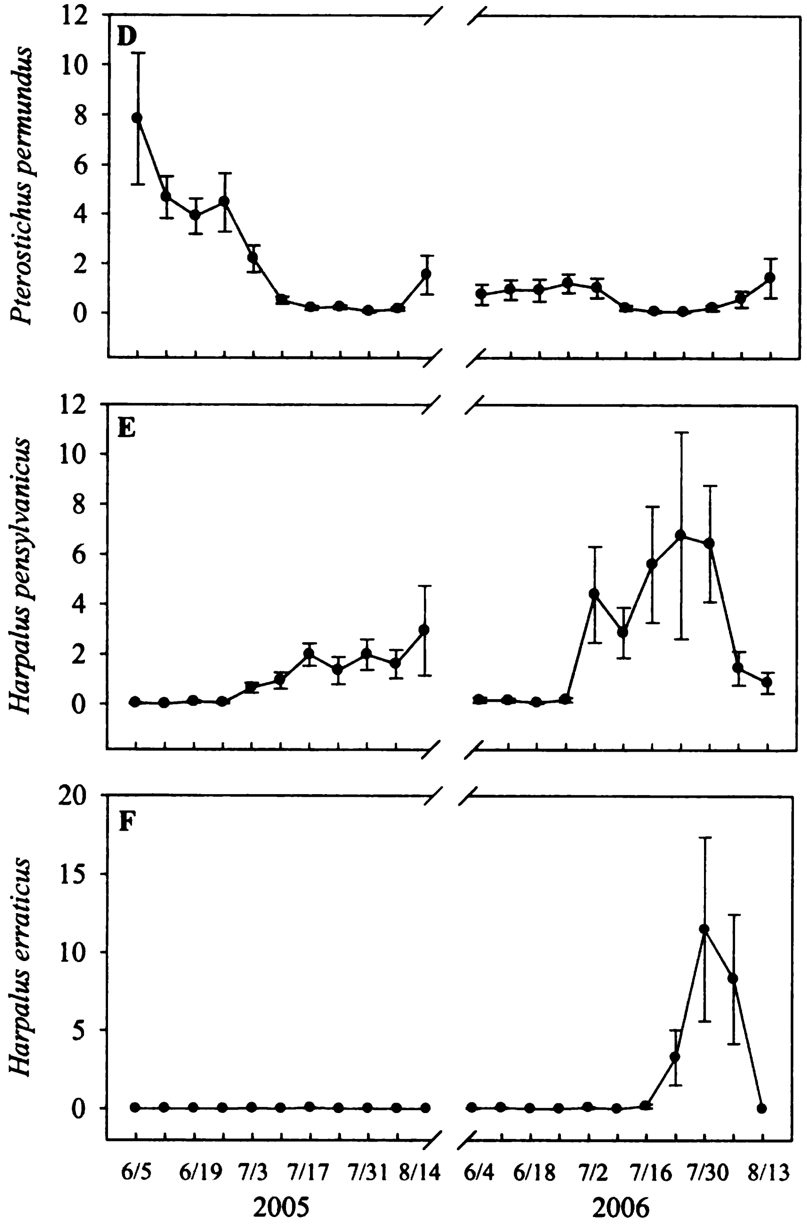


Figure 4.2 (continued)

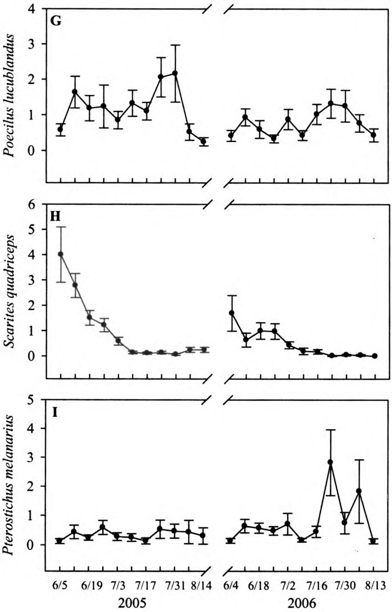


Figure 4.3.

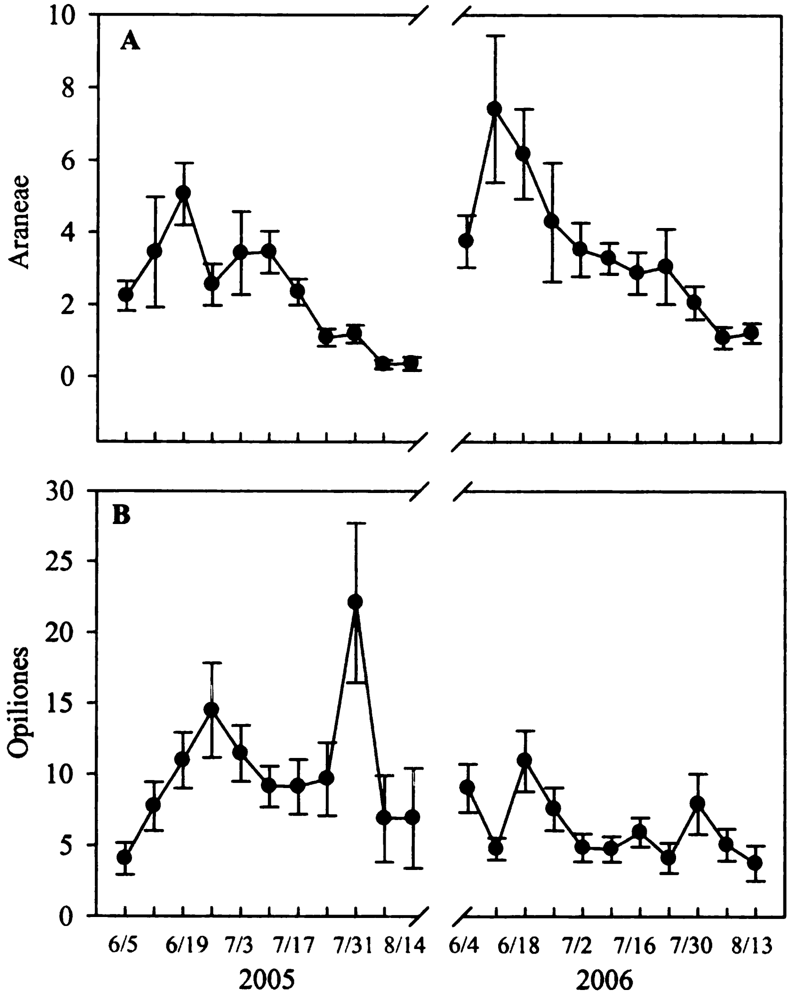


Figure 4.3. Activity density by date of (A) total Araneae (B) Opiliones, and the two most abundant families of Araneae: (C) Linyphiidae (see pg. 123), and (D) Lycosidae (see pg. 123) collected per pitfall trap for the 26 soybean fields sampled in 2005 and 2006.

Figure 4.3 (continued)

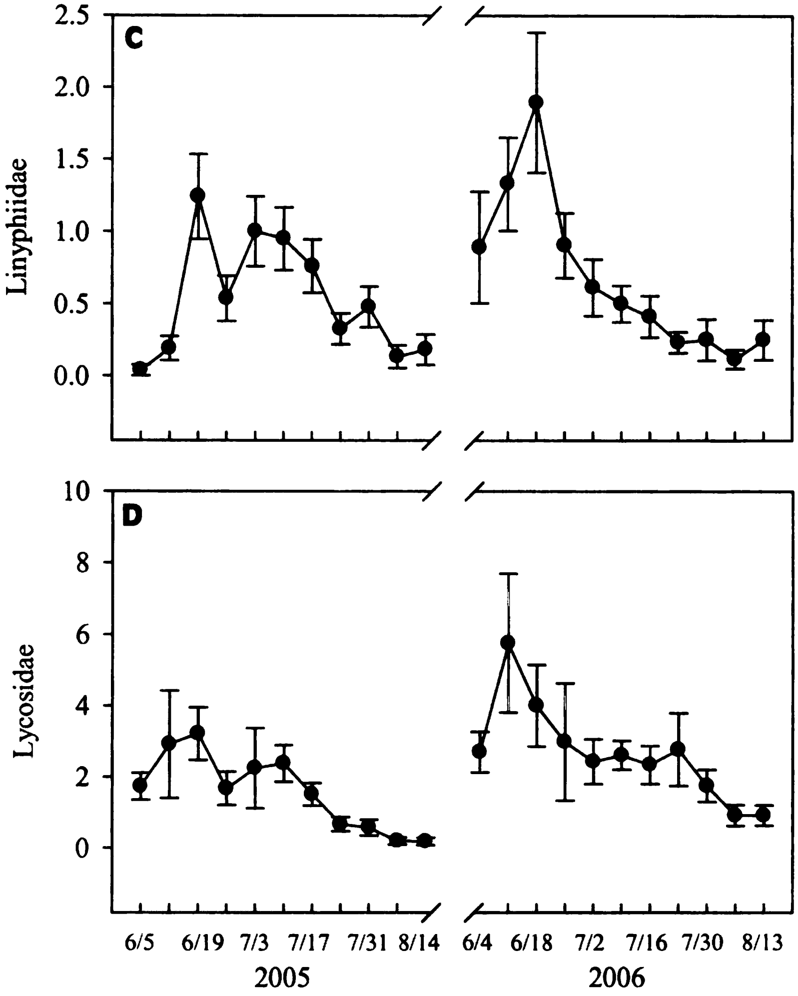


Figure 4.4.

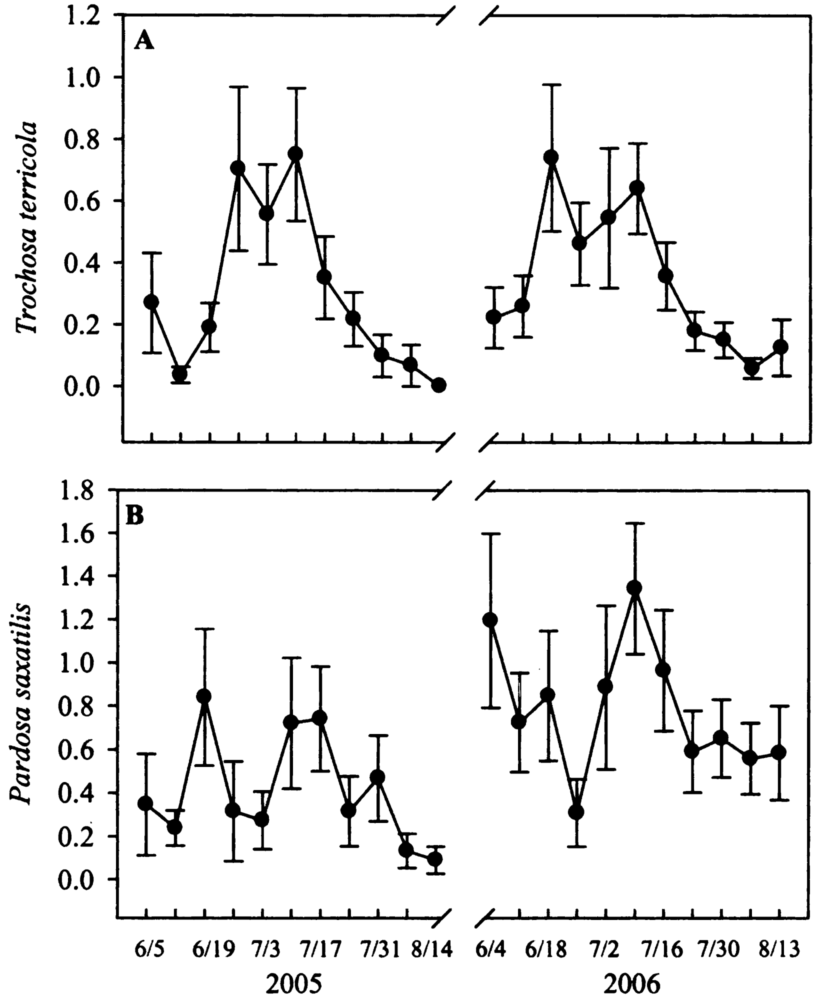


Figure 4.4. Activity density by date of the two most abundant species of Lycosidae (A) *T. terricola* and (B) *P. saxatilis* collected per pitfall trap for the 26 soybean fields sampled in 2005 and 2006.

Figure 4.5.

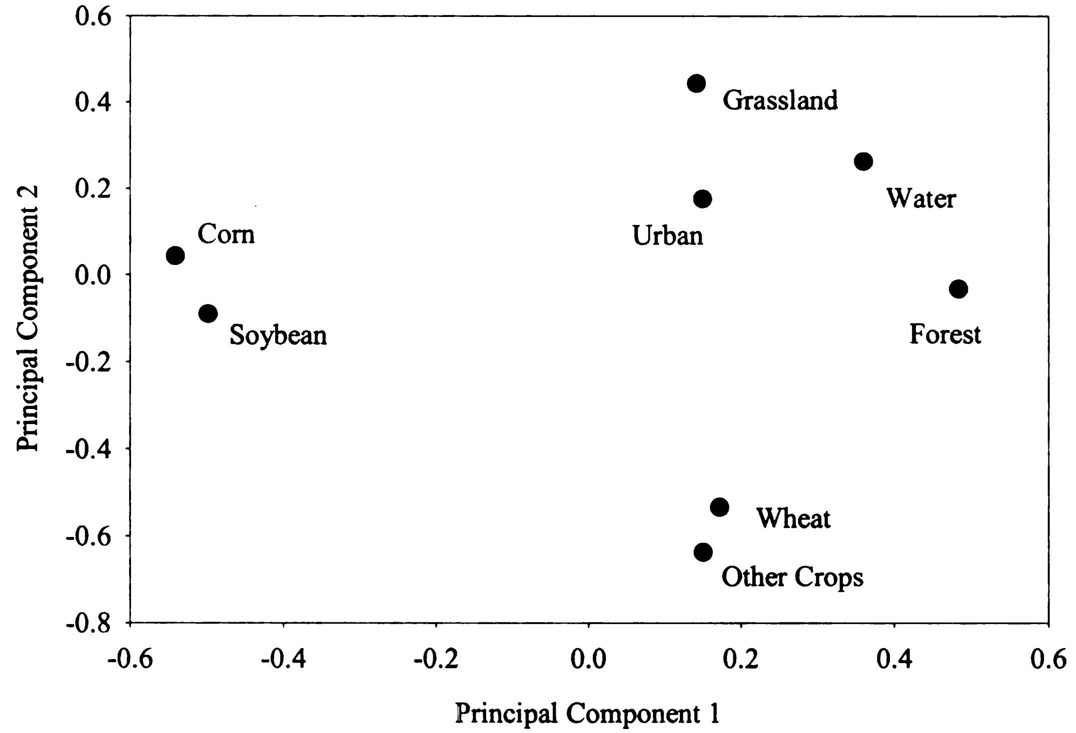


Figure 4.5. PCA ordination for principal components 1 and 2 of landscape elements surrounding soybean fields sampled. Data for a radius of 2 km is shown, plots are similar for all spatial scales. Sites with positive loadings on PC1 were correlated with the variable Forest while negatives loadings on PC1 were correlated with the variables Corn and Soybean. Sites with positive loadings on PC2 were correlated with the variable Grassland while negative loadings on PC2 were correlated with the variables Other Crops and Wheat.

Figure 4.6.

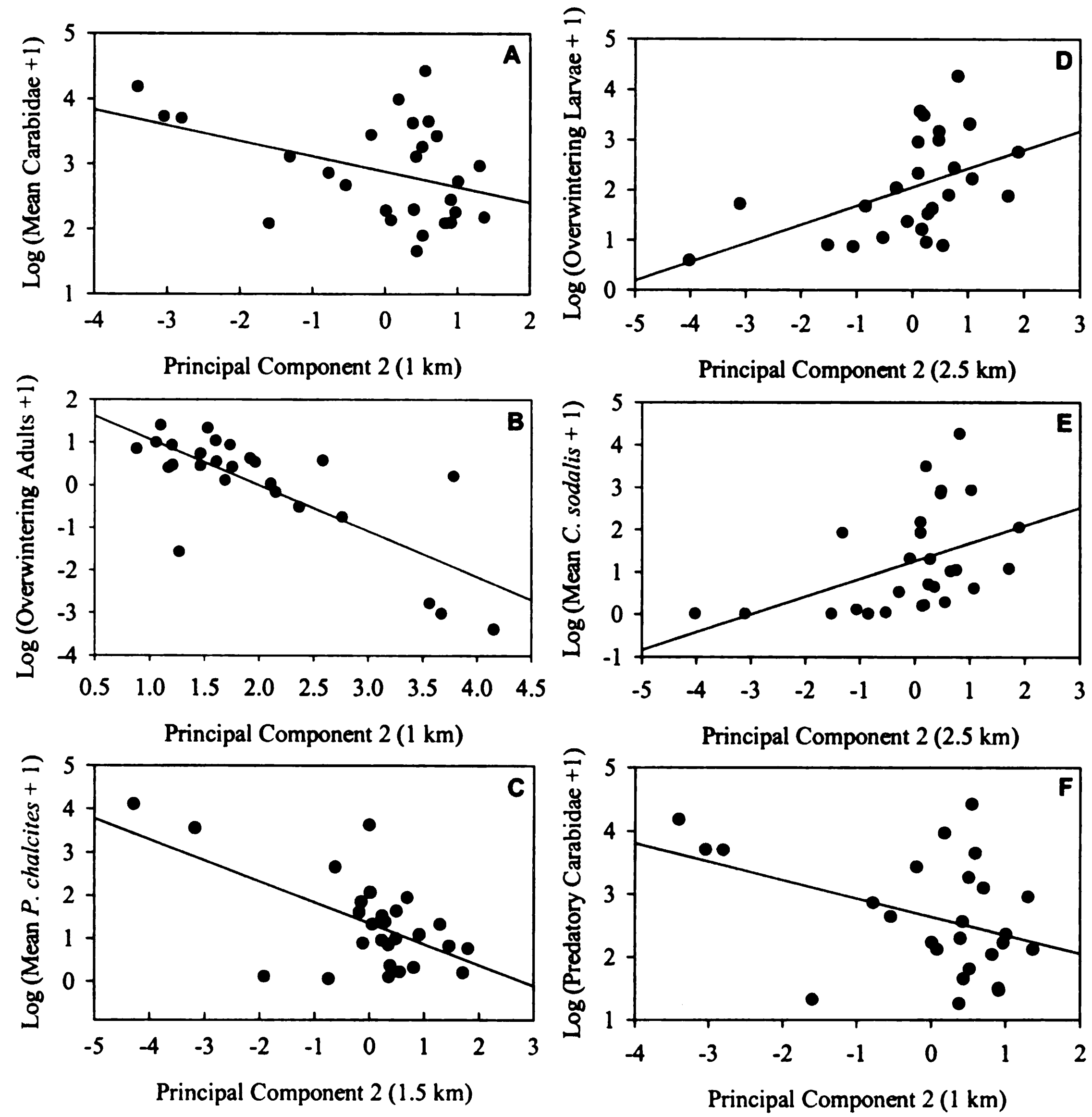


Figure 4.6. Relationship between (A) activity density of Carabidae and PC2 at 1 km, (B) adult-overwintering Carabidae and PC2 at 1 km, (C) *P. chalcites* and PC2 at 1.5 km, (D) larval-overwintering Carbidae and PC2 at 2.5 km, (E) *C. sodalis* and PC2 at 2.5 km, and (F) predatory Carabidae and PC2 at 1 km. Carabidae data were collected using pitfall traps. Means are log (x+1) transformed.

Figure 4.7.

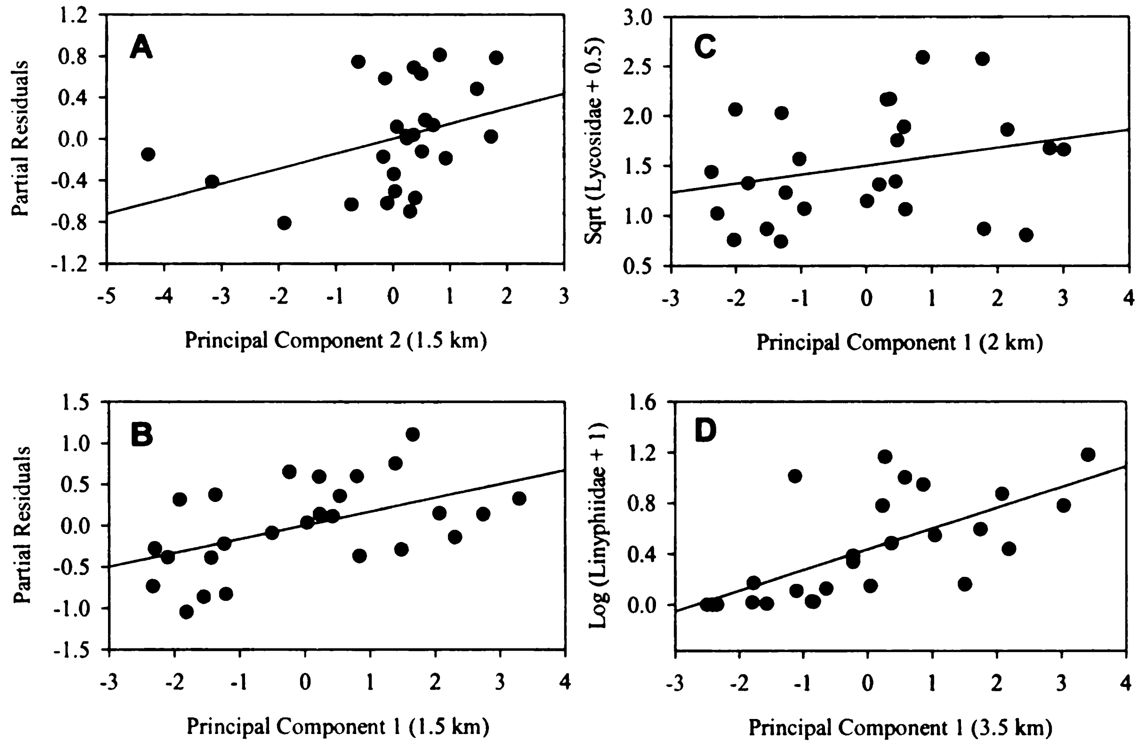


Figure 4.7. (A and B) Araneae activity density in 26 soybean fields was best explained by a model containing both PC1 and PC2 at a radius of 1.5 km. Partial residual plots illustrate a positive correlation with both PC1 and PC2. Plots (C) and (D) illustrate the relationship between Lycosidae activity density and PC2 at 2.5 km, and the relationship between Linyphiidae activity density and PC1 at 3.5 km respectively.

# CHAPTER 5

# LANDSCAPE COMPOSITION INFLUENCES PATTERNS OF NATIVE AND EXOTIC LADYBEETLE ABUNDANCE.

## Abstract

Landscape structure provides the foundation for species co-existence and resulting ecosystem services. Coccinellid beetles are important predators contributing to pest suppression in agricultural landscapes. Since the introduction of the exotic coccinellids *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas into the U.S., several studies have reported a decline of native Coccinellidae in agroecosystems. As part of a two-year study on the biological control of the soybean aphid, *Aphis glycines* Matsumura, I examined coccinellid communities in soybean fields across Michigan, Wisconsin, Minnesota and Iowa. In 2005-06, exotic species made up 90% of the total coccinellid community in Michigan soybean fields followed by Wisconsin (84%), Minnesota (66%) and Iowa (57%). *Harmonia axyridis* was the dominant exotic coccinellid in all states comprising 45-62% of the total coccinellid community, followed by *C. septempunctata* (13-30%). Two additional exotic species, *Hippodamia variegata* (Goeze) and *Propylea quatuordecimpunctata* (L.) were also discovered to be established in the region. Overall, the most abundant native coccinellid was *Hippodamia convergens* Guerin-Meneville, however, its abundance varied across the region, comprising 0% (Michigan) to 28% (Iowa) of the total coccinellid community. This is the first study to illustrate that patterns of native and exotic coccinellid abundance are influenced by

landscape structure. I found that native coccinellids were most abundant in low-diversity landscapes with an abundance of grassland habitat while exotic coccinellids were associated with the abundance of forested habitats. I propose that grassland dominated landscapes with low structural diversity and low amounts of forested habitat may be resistant to exotic coccinellid build-up, particularly *H. axyridis*, and therefore represent landscape-scale refuges for native coccinellid biodiversity.

## Introduction

Across the majority of the north central U.S. agricultural ecosystems form a human-mediated landscape matrix containing small patches of formerly dominant natural habitats. These natural habitats may serve as source populations of organisms which colonize the highly disturbed matrix, influencing the abundance of pest and beneficial insects and the ecosystem services such as biocontrol and pollination they provide in croplands (Marino and Landis 1996, Menalled et al. 1999, Ostman et al. 2001, den Belder et al. 2002, Steffan-Dewenter et al. 2002, Thies et al. 2003, Thies et al. 2005, Tscharntke et al. 2005b, Marino et al. 2006, Westphal et al. 2006, Gardiner et al. *in press*). Landscapes supply both native and exotic species to agricultural ecosystems resulting in agricultural food webs containing intentionally and unintentionally introduced species at each trophic level. Although it is well established that the two largest threats to native biodiversity are a loss of habitat and the introduction of exotic species, (Wilcove et al. 1998) very little is known regarding how the amount of natural habitat remaining in a landscape influences the abundance of native species and their exotic competitors within the agricultural landscape matrix. Didham et al. (2007) found that of 11,588 studies that examined the influence of land-use change and 3,528 studies that examined the effects of invasion published between 2002 and 2007 only 1.2 % considered both potential impacts on native biodiversity. From both a conservation and ecosystem services perspective, it is critical to determine how both of these factors influence populations of natives species. Herein, I investigate the influence of landscape composition on populations of declining native Coccinellidae and their exotic competitors.

The use of exotic lady beetles in classical biological control projects was fueled by the success of the vedalia beetle, *Rodalia cardinalis* (Mulsant), introduced from Australia to suppress populations of the cottony cushion scale, *Icerya purchasi* Maskell, in 1889. Since this early biological control effort, over 100 species of exotic lady beetles have been either intentionally or accidentally released into North America (Harmon et al. 2007). Although the majority of introduced exotics have not significantly affected native communities, a small number successfully established throughout the U.S. have been implicated as contributing to native coccinellid decline. The two most prominent of these are *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas. Intentional introductions of *C. septempunctata* began in 1958, and over the next few decades beetles were released in several states (Schaefer et al. 1987). This species was first detected in 1973 in New Jersey and Quebec, however, it remains unknown whether these established populations were the result of intentional or accidental introduction (Schaefer et al. 1987). *Harmonia axyridis* was first detected in the U.S. in 1988 (Chapin and Brou 1991). Like *C. septempunctata*, this species was intentionally released; but its eventual establishment has been attributed to an accidental introduction via shipping (Day et al. 1994). In the north-central U.S. two additional exotic species have been detected recently; *Propylea quatuordecimpunctata* (L.) (Gardiner et al. *in press*), and *Hippodamia* *variegata* (Goeze) (Gardiner and Parsons 2005). Both species were released as part of an effort at biological control of the Russian wheat aphid (Ellis et al. 1999).

Although exotic coccinellid species contribute to biological control of agricultural pests (Cardinale et al. 2003, Snyder and Evans 2006, Costamagna and Landis 2007a, Gardiner and Landis 2007) increasing evidence suggests that some species of exotic lady beetles may also displace native coccinellid species (Putnam 1955, Wheeler and Hoebeke 1995, Elliott et al. 1996, Colunga-Garcia and Gage 1998, Michaud 2002, Alyokhin and Sewell 2004, Snyder et al. 2004a, Harmon et al. 2007). Putman (1955) was one of the first to document this phenomenon, indicating that introduction of *Stethorus punctillus* Weise resulted in the displacement of the native *Stethorus punctum* (LeConte) in orchards on the Niagara Peninsula. Wheeler and Hoebeke (1995) attributed the decline of *Coccinella novemnotata* Herbst to an increase of *C. septempunctata* in the northeastern U.S. Once common, only 10 specimens of *C. novemnotata* have been collected in North America in the last 10 years (Losey et al. 2007). A similar pattern was documented in South Dakota by Elliott et al. (1996) who attributed a 20-fold reduction in populations of *Coccinella transversoguttata richardsoni* Brown and *Adalia bipunctata* (L.) to the establishment of *C. septempunctata*. Colunga-Garcia and Gage (1998) reported a decrease in populations of *Brachiacantha ursina* (F.), *Cycloneda munda* (Say), and *Chilocorus stigma* (Say) following the establishment of *H. axyridis* in Michigan. Similarly, Alyokhin and Sewell (2004) found a significant decline in *C. transversoguttata* and *Hippodamia tredecimpunctata* (Say) in Maine potato fields following the invasion by exotic lady beetles. The introduction of *H. axyridis* has also been reported to have led to a decline in other exotic species. Brown and Miller (1998) found that *C. septempunctata* declined in apple orchards in West Virginia following the establishment of *H. axyridis*.

Like many natural enemies, adult coccinellids are transient predators, foraging within several habitats during the growing season (Evans 2003). Therefore, their diversity and abundance is likely to depend on both the abundance of prey within crop habitats and the structure and composition of the surrounding landscape (Marino and Landis 1996, Colunga-Garcia et al. 1997, Bommarco 1998, Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharntke 2005, Tscharntke et al. 2005b, Gardiner et al. *in press*). Landscape variables such as habitat composition, quality, and patchiness as well as dispersal capability, all impact the abundance of coccinellids in agricultural crops (Elliott et al. 1999, Thies et al. 2003, Schmidt and Tscharntke 2005). Agroecosystems are ephemeral habitats where disturbances such as tillage, pesticide application and harvesting require both pests and their natural enemies to frequently re-colonize fields (Wissinger 1997). The surrounding landscape supplies a species pool of these organisms, and may impact the invasion success of exotic coccinellids as well as interactions between native and exotic coccinellid species.

Several recent studies show that coccinellids supply a valuable ecosystem service to soybean farmers, suppressing populations of the soybean aphid, *Aphis glycines* Matsumura, an invasive pest of soybean in the U.S. (Venette and Ragsdale 2004, Fox et al. 2005, Costamagna and Landis 2007a, Gardiner and Landis 2007, Gardiner et al. *in press,* Chacon et al. *in review*). Given the patterns of native species decline, and the importance of landscape diversity and composition in supplying beneficial insects to croplands, I was interested in determining if soybean fields in landscapes that varied in diversity and composition were colonized by a similar community of coccinellids. My objectives were to: 1) measure variation in the composition of the coccinellid community across the north-central states of Iowa, Michigan, Minnesota and Wisconsin 2) determine if the abundance of native and exotic coccinellids was related to the diversity and composition of the surrounding landscape. My hypothesis was that landscapes with a high proportion of natural habitat such as forests and grasslands would supply the largest population of coccinellids to soybean fields.

## Methods

### *Field sites*

Between June and August of 2005 and 2006, I examined the abundance of exotic and native coccinellids in 33 soybean fields in Iowa, Michigan, Minnesota, and Wisconsin (Figure 5.1). Twenty-two sites were part of a USDA Risk Avoidance and Mitigation (RAMP) funded multi-state study of soybean aphid management. In each RAMP site a randomized complete block design with 4-6 blocks and either 4 (2005) or 5 (2006) treatments was established in 0.4 ha (2005) or 0.2 ha (2006) plots. Multiple experiments occurred within these fields; with the study reported here was conducted in control plots not treated with insecticide. An additional 11 sites included in this study were commercial production fields (2 in 2005 and 9 in 2006), each containing four 0.4 ha (2005) or 0.2 ha (2006) untreated plots. Each year, a minimum distance of 20 km separated each site. Across years, I maintained the relative regional distribution of soybean fields, but sampled different sites. The average distance between soybean sites sampled in 2005 or 2006 within a given region was 2.4 km (range = 0.2-14.6 km, Figure 1). Field size averaged 16.0 ha (range = 13.6-48.1 ha).

*Aphid and coccinellid sampling*

Beginning in June of 2005 and 2006 and continuing until mid to late August, coccinellid diversity and abundance was estimated by placing an unbaited yellow sticky card (PHEROCON AM, Great Lakes IPM, Vestaburg, MI) in each plot at all study sites (4 cards per site in both 2005 and 2006). Yellow sticky card traps have been shown to be an effective sampling technique for coccinellids in croplands, with greater capture efficiency than other sampling techniques such as visual plant counts or vacuum sampling (Mensah 1996, Parajulee and Slosser 2003, Schmidt et al. 2008a). In the center of each plot, a metal "T" fence post was erected with holes every 10 cm vertically. A 0.61 cm diameter dowel was placed through a hole such that it suspended a 22.9 x 27.9 cm sticky card just above the plant canopy. As plants grew, the dowel was moved up the post to keep the trap just above canopy level. Sticky traps were replaced every 7 days. All adult coccinellids were counted and identified to species. The number of exotic and native coccinellids found per sticky trap was averaged across all sampling dates for each site. As soybean aphid populations varied across the study region, I also measured prey availability as a potential predictor of coccinellid abundance by conducting weekly destructive whole plant counts during the timeframe of the coccinellid sampling. In each plot, five randomly selected plants were removed from the ground and the number of apterous and alate aphids were counted on each plant. For analysis, prey abundance was averaged across all sampling dates for each site.

*Landscape analysis*

Field geospatial data was collected using a handheld GPS receiver using Wide Area Augmentation System (WAAS) correction. The spatial coordinate for the center of each site was used to obtain ortho-rectified digital aerial imagery. I digitized the habitats surrounding each study site to a radius of 3.5 km using ARC GIS 9.1. Aerial images were captured between 1998 and 2006. Land use changes between the image date and study period were recorded by ground-verification in June – August annually, with corrections made during the digitization process. At the same time, I also determined the specific land cover (n = 25 categories) present in all areas of each landscape (Table 5.1). Some locations included polygons that were not visible from a roadway and permission to access private lands could not always be obtained. These polygons were given a value of zero and were excluded from further analysis. The area of each site that could not be identified varied from 0-4.5%. The smallest polygons identified included field plots on university research farms and small patches of fallow field (< 5 $m^2$); the largest were contiguous urban areas, lakes, and forests (< 11.9 $km^2$).

Landscape diversity was measured using Simpson's Index (D) (Simpson 1949). Simpson's Index is typically used to examine the variance of species abundance distributions. Here I applied it to examine variance in the proportion of area covered by each of 25 land use categories. This index was calculated for each of the landscapes at each of the spatial scales examined. The equation for Simpson's Index (D) is: $D = 1/\sum(p_i)^2$ where $p_i$=proportion of habitat in the $i^{th}$ land-cover category (D increases as diversity increases). Using methods modeled after Thies et al. (2003), I measured landscape diversity at 6 spatial scales ranging from 1 km to 3.5 km radii (at 0.5 km intervals) from the field center.

*Statistical analysis*

To examine variation in coccinellid communities found in Iowa, Michigan, Minnesota and Wisconsin I first performed a likelihood ratio chi square analysis assuming a multinomial distribution (Shao 2003). This test compared the proportion of the coccinellid community composed of individual species at the state level across both 2005 and 2006 to determine if the coccinellid community within each state is significantly different from the null hypothesis that the proportional distribution is equivalent across all four states.

To evaluate the relationship between coccinellid abundance and landscape variables, I performed a principal components analysis (PCA) on the landscape variables in order to reduce the dimensions of the data. The 25 observed land cover categories were combined into seven variables included in the PCA: four crop variables and three non-crop (Table 5.1). The four crop variables included the three most abundant crops as separate categories: Corn, Soybean, and Wheat. The fourth variable was "Other Crops" which included all other crops planted within a 3.5 km radius of our soybean sites. This included many regionally-important and small acreage specialty crops. The three non-crop variables were Forest, Grassland, and Urban. The Forest variable included all forested land, the majority of which was deciduous forest. Some landscapes also included small acreage of planted coniferous stands as well as mixed stands of conifers and deciduous trees. The Grassland variable included all perennial habitat lacking dominant woody vegetation. This included old field and restored prairie, grazed pasturelands and forage crops. The final non-crop variable was Urban which included residential and urban areas. The water and wetlands variable was dropped from the principal components analysis as this habitat constituted a low (< 2%) percentage of the majority of landscapes. Principal component axes were extracted using correlations among variables and the resulting factors were not rotated (McCune and Mefford 1999). I restricted the analysis to the first two eigenvectors which explained between 51.3-57.3% of the variability in landscape data. This was done for each spatial scale (1.0-3.5 km radii).

Akaike's Information Criterion was used as a model selection procedure to examine the influence of six variables on the abundance of native and exotic Coccinellidae. These variables were: Year (year site was sampled, 2005 or 2006), Prey (average abundance of soybean aphid present in each site), Exotic (average abundance of exotic Coccinellidae present in each site, used only in native Coccinellidae models), D (Simpson's Diversity (D)), PC1 (principal components 1 interpreted from PCA), and PC2 (principal component 2 interpreted from PCA) (Table 5.1). For exotic coccinellids 17 models were compared: an intercept only model, sampling year model and models containing all combinations of the two interpreted principal components, Simpson's D, and prey abundance (Table 5.2). For native coccinellids, 33 models were compared, including an intercept only model, sampling year model, and models containing all combinations of the two interpreted principal components, Simpson's D, prey abundance, and exotic coccinellid abundance (Table 5.1). At each spatial scale I present the model with the minimum AICc value, i.e. with the best support for the data, and any competing models with a AICc difference of less than two (Ribic and Sample 2001, Burnham and Anderson 2002). For each model, I present the maximum log-likelihood estimate, the Akaike weights, which estimate the relative likelihood of a given model against all other models, and AICc differences ($\Delta_i$). I calculated adjusted $r^2$ for the minimum AICc model and competing models to evaluate how well the models explained the variation in the data. I define the best overall model as the model with the lowest AICc score across all spatial scales. After determining the best overall model for each predictor, I examined the relationship between this model and the two most abundant species of native or exotic coccinellids. I calculated partial correlations for all variables in models with more than one predictor. Partial correlations were used to assess the importance of individual independent variables after adjusting for additional variables in the model. The $AIC_c$ analysis and adjusted $r^2$ were determined using R version 2.1.1 (R Development Core Team 2005). Partial correlations were obtained using PROC CANCORR in SAS v. 9.1 (SAS Institute 1999). The mean number of native and exotic coccinellids, mean numbers of individual coccinellid species as well as mean prey abundance were log (x+1) transformed prior to analysis to meet the assumptions of normality and homogeneity of variances (SAS Institute, 1999).

While no site had an overlapping 3.5 km landscape buffer within a given year, 24 sites did have overlapping buffers across years. Therefore, prior to interpreting the results of the $AIC_c$ analysis, I examined potential spatial autocorrelation of the residuals of the best fit and competing models for both response variables (exotic and native Coccinellidae). This was done between each site and the nearest neighboring site using Moran's I statistic. I did not find evidence of spatial autocorrelation between neighboring sites for any of the best fit or candidate models examined for either response variable.

## Results

*Coccinellid diversity and abundance across the region*

Four exotic and eight native species of coccinellids were observed on sticky cards in 2005 and 2006 (Table 2) across the study area in the north-central U.S. There were significant differences in the composition of this community across the four states ($X^2_{24}$= 756.34, P<0.0001). Michigan had the highest percentage of exotic coccinellids (90.0%) followed by Wisconsin (84.3%) (Table 5.3). Exotic species were less dominant in Minnesota and Iowa, comprising (65.6%) and (57.2%) of the coccinellid communities respectively. In all four states, the most abundant exotic species was *H. axyridis* followed by *C. septempunctata*. Two additional exotic species were detected: *H. variegata* in Michigan and Wisconsin and *P. quatuordecimpunctata* in Michigan (Gardiner and Parsons 2005, Gardiner et al. *in press*).

The most abundant native species was *Hippodamia convergens* Guerin-Meneville, which comprised a greater proportion of the community in Iowa (28.3%) and Minnesota (19.5%) compared to Michigan (0%) and Wisconsin (4.9%). The second most abundant native species was *C. maculata* which comprised 2.2-6.2% of the coccinellids detected in soybean fields (Table 5.3).

*Landscape diversity*

The landscape surrounding each of the field sites varied from agriculturally-dominated to forest and grassland-dominated. Within the 3.5 km landscape radius surrounding each of the 33 sites, landscape diversity values (D) ranged from 2.4-6.4. The percentage of the landscape composed of annual cropland ranged from 11-91%. Landscapes with high and low percentages of annual cropland were sampled in each state

(Michigan 11- 91%, Wisconsin 20-71%, Minnesota 44-84%, and Iowa 27-89%). At a 3.5 km radius grassland habitat comprised 1-69% (Michigan 1-21%, Wisconsin 4-21%, Minnesota 6-18%, and Iowa 5-69%) while forested habitat comprised 0-58% of the landscape surrounding field sites (Michigan 3-32%, Wisconsin 3-58%, Minnesota <1-16%, and Iowa 0-6%)

### *Principal component analysis of landscape variables*

Both of the principal components interpreted in this study were measures of landscape composition (Figure 5.2). PC1 was correlated with the variable Forest while negatives loadings on PC1 were correlated with the variables Corn and Soybean. Therefore sites with positive values of PC1 suggest a landscape with an abundance of wooded habitat while sites with negative values of PC1 indicate a landscape dominated by corn and soybean agriculture (Figure 5.2). For PC2, sites with positive loadings were correlated with the variable Grassland and negative loadings were correlated with the variables Other Crops and Wheat. Sites with high values of PC2 had a high proportion of pastures, old fields, and restored prairies. Sites with negative values had a high proportion of locally important fruit, vegetable, ornamental and small grain crops. Both principal components indicate the intensity of landscape disturbance, with high values indicating less disturbed grassland and forested habitats and low values indicating greater agricultural disturbance.

### *Model fitting of relationships between coccinellid abundance, prey and landscape variables*

For exotic coccinellids, the PC1 model had the lowest AICc value and the PC1+Prey model was a competing model at all spatial scales examined (radii of 1-3.5

km) (Table 5.4). The PC1 model at 2 km was the best fit model overall, with the lowest AICc value across spatial scales. PC1 was a significant predictor of exotic coccinellid abundance (*P* = 0.003, 2 km). Exotic coccinellid abundance was highest in soybean fields in landscapes with an abundance of forested habitat (Figure 5.3a). The two most abundant species of exotic coccinellid both increased with PC1. This relationship was statistically significant for *H. axyridis* (*P* = 0.004, 2 km) but not for *C. septempunctata* (*P* = 0.139, 2 km) (Figure 5.3b-c). In the competing PC1+Prey model, prey abundance was not a significant predictor of exotic coccinellid abundance (*P* = 0.209, 2 km) but was for *H. axyridis* (*P* = 0.022, 2 km), which increased with soybean aphid populations. There was not a significant correlation between *C. septempunctata* and prey abundance in the PC1+Prey model (*P* = 0.475, 2 km) (Figure 5.3d-f).

For native coccinellids, the best fit and candidate models varied by spatial scale. The Year model had the lowest AICc value at spatial scales of 1-1.5 km, while at radii of 2-3.5 km the Diversity+PC2 model had the lowest AICc value. Several competing models were found across spatial scales including: Year, PC2, Diversity, Diversity+PC2, PC1+PC2, PC2+Exotic, and Diversity+PC2+Exotic. The Diversity+PC2 model at 2 km had the lowest AICc value across spatial scales. Native species were significantly correlated with both predictors in this model; being most abundant in low diversity landscapes (Diversity, *P*=0.043 at 2 km) with an abundance of grassland (PC2, *P*=0.038 at 2 km) (Figure 5.4 a and d). The most abundant native coccinellid species, *H. convergens* was also significantly correlated with both variables included in the best fit model. This species was also most abundant in low diversity landscapes (Diversity, *P*=0.024 at 2 km) with an abundance of grassland (PC2, *P*=0.024 at 2 km) (Figure 5.4 b and e). There was not a significant correlation between the second most abundant native coccinellid, *C. maculata* and any of the variables in the best fit model (Figure 5.4 c and f).

## Discussion

Over the past 100 years the proportion of native coccinellids found in lady beetle communities has declined dramatically (Harmon et al. 2007), primarily since the mid 1980's. Harmon et al. (2007) stated that in studies between 1914-1985, native species averaged 95% of all coccinellid individuals found, while between 1987-2001 natives declined to 67.5%. Several authors concluded that this decline in native species abundance is tied to the establishment of exotic coccinellids (Putnam 1955, Wheeler and Hoebeke 1995, Elliott et al. 1996, Michaud 2002, Evans 2004, Snyder et al. 2004a, Snyder and Evans 2006, Harmon et al. 2007). Here, I investigated the influence of landscape structure on the abundance of both native and exotic coccinellid populations across Iowa, Michigan, Minnesota, and Wisconsin. I found that coccinellid populations in soybean fields across a 4-state region varied significantly in diversity and abundance. The proportion of the lady beetle community comprised of native species in soybean increased from Michigan (10.0%) west to Iowa (44.8%). In all states, *H. axyridis* was the most abundant exotic species, followed by *C. septempunctata*. The most abundant native species in Wisconsin, Minnesota, and Iowa was *H. convergens*. This species was not detected in any of the 14 Michigan soybean fields sampled, although it was documented by previous investigators in soybean in recent years (Fox et al. 2005, Costamagna and Landis 2007a).

### *Native and exotic coccinellid populations in soybean fields*

This study illustrates that temporal, within-field, and landscape variables all influence the abundance of coccinellids in soybean fields. Year was a significant predictor of native coccinellids with populations higher in 2005 than 2006. I did not see a significant correlation between the within-field average soybean aphid abundance and trap catches of native Coccinellidae, however, yearly differences may be tied to variation in the abundance of *A. glycines* across the study region. On average, soybean aphid was more abundant in 2005 compared with 2006 across the four states studied. Fields with particularly high aphid populations may have acted as sources of native species, resulting in greater foraging across the landscape. An alternative explanation for the significant year effect is the positive correlation between the abundance of *H. axyridis* and soybean aphid. This coccinellid is important in the biological control agent of *A. glycines* (Gardiner and Landis 2007) and may act as more of an *A. glycines* specialist than the other coccinellids sampled. Increases in populations of this species with soybean aphid may have led to greater intraguild predation pressure on native species in late 2005, reducing overwintering and 2006 populations.

Landscape variables were also significant predictors of native and exotic coccinellid populations. Landscapes with an abundance of forested habitat supported greater numbers of exotic coccinellids, particularly *H. axyridis*, in soybean fields. Soares et al. (2008) describe the "champion hypothesis" to describe the successful invasion of *H. axyridis*. This hypothesis states that morphological, physiological, and behavioral traits, including a large body size, high fecundity, high foraging efficiency and a high conversion efficiency of prey to biomass, lead to the success of *H. axyridis* throughout a large invaded range (Soares et al. 2008). While *H. axyridis* was present throughout the study region, I found it in significantly greater abundance in landscapes with an abundance of forested habitats. The forested habitats present in these landscapes are highly fragmented and intermixed within an agricultural matrix. This type of landscape supplies exotic ladybeetles with an abundance of habitat edge and variation in vertical structure which may favor species such as *H. axyridis* which is an arboreal species in its native range (Chapin and Brou 1991). This coccinellid is highly mobile and disperses in and out of forest patches throughout the growing season (Gardiner 2008). It also exhibits a hypsotactic behavior when searching for overwintering sites, flying to prominent objects in the landscape (Koch 2003) such as forest edges. I propose that a landscape lacking abundant forested habitat may limit the success of *H. axyridis* and potentially its impacts on native coccinellids.

This study illustrates that the abundance of native species in soybean fields is greatest in low diversity landscapes with an abundance of perennial grassland habitat. These include pasturelands, perennial forage crops, restored prairies, and old fields. I hypothesize that these perennial landscape elements are likely to provide early season prey and overwintering habitat for native species, while not supporting high populations of exotic competitors. These perennial habitats may serve as source populations of native species that disperse into annual cropping systems such as soybean embedded within the landscape. In addition to their association with grassland habitats, native coccinellid abundance was negatively correlated with landscape diversity (D). While seemingly counter-intuitive, landscapes with the highest values of Simpson's D were highly fragmented and contained high proportions of forested habitat, while grassland patches were frequently embedded in low diversity agricultural landscapes.

### *Coccinellidae and landscape scale*

I measured the response of coccinellid species to landscape structure at 6 spatial scales ranging from a 1-3.5 km radius from the focal soybean field. Season-long coccinellid populations were best predicted by the abundance of forests for exotic species and grasslands for native species at a radius of 2.0 km. These results are consistent with other studies examining the abundance of herbivores, natural enemies, and biocontrol services (Thies et al. 2003, Schmidt and Tscharntke 2005, Gardiner et al. *in press*). Gardiner et al. (*in press*) found that the amount of biocontrol services supplied by a landscape to soybean fields was correlated with increased landscape diversity at a radius of 1.5 km surrounding soybean fields. Thies et al. (2003) found that herbivory and parasitism in wheat fields were positively correlated with percent non-crop area at landscape diameter of 1.5 km.

### *Implications*

This study demonstrates that native and exotic coccinellids are favored by different types of landscapes, and that competitive and predatory interactions between these species may contribute to this partitioning. It is possible that native species like *H. convergens* and *C. maculata* may be adapted to open savanna and prairie landscapes that formerly dominated large areas of the north-central U.S. and may still favor landscapes with an abundance of open grassland and field crop habitat. However, this does not explain the decline in native coccinellids in the last few decades, long after landscapes were transformed by human settlement. Alternatively, native species may only be able to thrive in landscapes which are less favorable to invasion by exotic species many of which are known to be strong intraguild predators. If exotics are favored by forested habitat, a lack of these landscape elements in portions of Minnesota and Iowa may restrict the abundance and dominance of exotics in these areas. *Harmonia axyridis,* the most abundant exotic species found, was detected in 1994 in both Michigan and Iowa (Colunga-Garcia and Gage 1998, Rice 2006) therefore it does not appear that these differences are the result of an invasion front that has not yet fully colonized the western end of the study region. Instead, I propose that landscape structure may be limiting the success of *H. axyridis* and other exotics in intensely agricultural landscapes and allowing persistence of native coccinellid communities in such regions. If so, understanding the role of perennial grasslands in supporting source populations of native coccinellids is a conservation priority. Evans (2000) discussed the habitat compression hypothesis, where after the introduction of an exotic, native species decline in agricultural habitats as they must compete with exotics for prey. Natives are forced back into ancestral habitats where prey are sufficient to maintain populations (Evans 2000). We must determine if the different types of perennial grassland, such as pasturelands, restored prairies and abandoned old fields vary in their ability to support native species. Within these habitats, an understanding of the amount competitive displacement or intraguild predation pressure from exotics incurred by native populations will demonstrate which serve as important refuges in the conservation of these species.

Table 5.1. Land cover categories used in the calculation of Simpson's Diversity Index (D) and as variables included in the principal components analysis.

| Simpson's Diversity (D) | PCA |
|---|---|
| Cropland Categories | |
| Corn | Corn |
| Soybean | Soybean |
| Wheat | Wheat |
| Sugar Beet | Other Crops[1] |
| Dry Bean | |
| Tree Fruit | |
| Sunflower | |
| Cabbage | |
| Canola | |
| Potato | |
| Carrot | |
| Squash | |
| Strawberry | |
| Tomato | |
| Bell Peppers | |
| Melons | |
| Mint | |
| Ornamental and Rare Crops | |
| Tilled Field | |
| Non-Crop Categories | |
| Forage | Grassland[2] |
| Old Field and Restored Prairie | |
| Pastureland | |
| Forested | Forest |
| Wetlands and Open Water[3] | |
| Urban | Urban |

[1] Other Crops contains all Simpson's D cropland categories except corn, soybean, and wheat.

[2] Grassland contains the Simpson's D non-crop categories Forage, Old Field and Restored Prairie, and Pastureland

[3] Proportion Wetlands and Open Water was dropped from the PCA analysis due to rarity.

Table 5.2. Models compared by AICc analysis at spatial scales of 1.0-3.5 km.

| **Models for Exotic and Native Coccinellidae** | **Additional Models for Native Coccinellidae** |
|---|---|
| $B_0$ | $B_0 + B_1$Exotic[6] |
| $B_0 + B_1$Year[1] | $B_0 + B_1$D + $\mathrm{B}_2$Exotic |
| $B_0 + B_1$D[2] | $B_0 + B_1$PC1 + $\mathrm{B}_2$Exotic |
| $B_0 + B_1$PC1[3] | $B_0 + B_1$PC2 + $\mathrm{B}_2$Exotic |
| $B_0 + B_1$PC2[4] | $B_0 + B_1$PC1 + $B_2$PC2 + $B_3$Exotic |
| $B_0 + B_1$PC1 + $B_2$PC2 | $B_0 + B_1$D + $B_2$PC1 + $B_3$Exotic |
| $B_0 + B_1$D + $B_2$PC1 | $B_0 + B_1$D + $B_2$PC2 + $B_3$Exotic |
| $B_0 + B_1$D + $B_2$PC2 | $B_0 + B_1$D + $B_2$PC1 + $B_3$PC2 + $B_4$Exotic |
| $B_0 + B_1$D + $B_2$PC1 + $B_3$PC2 | $B_0 + B_1$Prey + $\mathrm{B}_2$Exotic |
| $B_0 + B_1$Prey[5] | $B_0 + B_1$D + $B_2$Prey + $B_3$Exotic |
| $B_0 + B_1$D + $B_2$Prey | $B_0 + B_1$PC1 + $B_2$Prey + $B_3$Exotic |
| $B_0 + B_1$PC1 + $B_2$Prey | $B_0 + B_1$PC2 + $B_2$Prey + $B_3$Exotic |
| $B_0 + B_1$PC2 + $B_2$Prey | $B_0 + B_1$PC1 + $B_2$PC2 + $B_3$ Prey + $B_4$Exotic |
| $B_0 + B_1$PC1 + $B_2$PC2 + $B_3$ Prey | $B_0 + B_1$D + $B_2$PC1 + $B_3$ Prey + $B_4$Exotic |
| $B_0 + B_1$D + $B_2$PC1 + $B_3$ Prey | $B_0 + B_1$D + $B_2$PC2 + $B_3$ Prey + $B_4$Exotic |
| $B_0 + B_1$D + $B_2$PC2 + $B_3$Prey | $B_0 + B_1$D + $B_2$PC1 + $B_3$ PC2 + $B_4$ Prey + $B_5$Exotic |
| $B_0 + B_1$D + $B_2$PC1 + $B_3$ PC2 + $B_4$Prey | |

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[1] Year = Year coccinellids were sampled, 2005 or 2006

[2] D = Simpson's Diversity where D = $1/\sum(\mathrm{pi})^2$ and pi=proportion of habitat in the ith land-cover category

[3] PC1 = Principal Component 1

[4] PC2 = Principal Component 2

[5] Prey = The average number of soybean aphids per plant within each site

[6] Exotic = The average number of exotic Coccinellidae within each site

Table 5.3. Coccinellid community composition in soybean fields in Iowa, Michigan, Minnesota and Iowa in 2005-2006.

| | Percent of Total Coccinellidae | | | | Mean Coccinellidae per Sticky Trap ± SEM | | | |
|---|---|---|---|---|---|---|---|---|
| | Iowa | Michigan | Minnesota | Wisconsin | Iowa | Michigan | Minnesota | Wisconsin |
| **Exotic Species** | | | | | | | | |
| *Harmonia axyridis* | 44.5 | 52.8 | 46.2 | 61.5 | 0.83 ± 0.07 | 0.98 ± 0.07 | 0.68 ± 0.10 | 1.29 ± 0.12 |
| *Coccinella septempunctata* | 12.8 | 30.0 | 19.5 | 22.6 | 0.24 ± 0.03 | 0.55 ± 0.05 | 0.29 ± 0.05 | 0.47 ± 0.06 |
| *Hippodamia variegata* | 0 | 5.57 | 0 | 0.20 | 0 | 0.10 ± 0.02 | 0 | 0.004 ± 0.004 |
| *Propylea quatuordecimpunctata* | 0 | 1.59 | 0 | 0 | 0 | 0.03 ± 0.01 | 0 | 0 |
| **All Exotic Species** | **57.2** | **90.0** | **65.6** | **84.3** | **1.08 ± 0.07** | **1.65 ± 09** | **0.97 ± 0.11** | **1.75 ± 0.14** |
| **Native Species** | | | | | | | | |
| *Hippodamia convergens* | 28.3 | 0 | 19.5 | 4.9 | 0.53 ± 0.06 | 0 | 0.29 ± 0.06 | 0.10 ± 0.02 |
| *Coleomegilla maculata* | 5.1 | 5.6 | 6.2 | 2.2 | 0.10 ± 0.02 | 0.10 ± 0.02 | 0.09 ± 0.03 | 0.05 ± 0.02 |
| *Hippodamia parenthesis* | 3.0 | 0.9 | 3.1 | 4.5 | 0.06 ± 0.01 | 0.02 ± 0.01 | 0.05 ± 0.02 | 0.09 ± 0.02 |
| *Hippodamia tridecimpuncata* | 0.4 | 0.3 | 1.0 | 3.7 | 0.01 ± 0.003 | 0.01 ± 0.003 | 0.02 ± 0.01 | 0.08 ± 0.05 |
| *Cycloneda munda* | 4.8 | 2.6 | 4.6 | 0.4 | 0.09 ± 0.01 | 0.05 ± 0.01 | 0.07 ± 0.02 | 0.01 ± 0.01 |
| *Chilocorus stigma* | 0 | 0.6 | 0 | 0 | 0 | 0.01 ± 0.01 | 0 | 0 |
| *Anatis labiculata* | 0.5 | 0 | 0 | 0 | 0.01 ± 0.01 | 0 | 0 | 0 |
| *Brachiacantha ursine* | 0.7 | 0.1 | 0 | 0 | 0.01 ± 0.01 | 0.002 ± 0.002 | 0 | 0 |
| **All Native Species** | **44.8** | **10.0** | **34.4** | **15.7** | **0.81 ± 0.07** | **0.33 ± 0.06** | **0.51 ± 0.08** | **0.33 ± 0.06** |
| **Total Coccinellidae** | | | | | **1.88 ± 0.10** | **1.82 ± 0.09** | **1.47 ± 0.14** | **2.08 ± 0.16** |

Table 5.4. Summary of model selection statistics for evaluating the abundance of exotic Coccinellidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1] [2] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 1.0 km | $B_0 + B_1\text{PC1}^{\dagger}$ | -5.75 | 3 | 18.34 | 0.00 | 0.23 | 0.13 | |
| 1.0 km | $B_0 + B_1\text{PC1}^{\dagger} + B_2\text{Prey}$ | -4.52 | 4 | 18.48 | 0.14 | 0.22 | 0.17 | PC1 = 0.43, Prey = 0.27 |
| 1.5 km | $B_0 + B_1\text{PC1}^{\dagger}$ | -4.55 | 3 | 15.94 | 0.00 | 0.30 | 0.19 | |
| 1.5 km | $B_0 + B_1\text{PC1}^{\dagger\dagger} + B_2\text{Prey}$ | -3.46 | 4 | 16.36 | 0.42 | 0.24 | 0.22 | PC1 = 0.49, Prey = 0.25 |
| **2.0 km** | $\boldsymbol{B_0 + B_1\text{PC1}^{\dagger\dagger}}$ | **-3.73** | **3** | **14.30** | **0.00** | **0.35** | **0.23** | |
| 2.0 km | $B_0 + B_1\text{PC1}^{\dagger\dagger} + B_2\text{Prey}$ | -2.85 | 4 | 15.14 | 0.84 | 0.23 | 0.25 | PC1 = 0.52, Prey = 0.23 |
| 2.5 km | $B_0 + B_1\text{PC1}^{\dagger\dagger}$ | -4.15 | 3 | 15.14 | 0.00 | 0.35 | 0.21 | |
| 2.5 km | $B_0 + B_1\text{PC1}^{\dagger\dagger} + B_2\text{Prey}$ | -3.31 | 4 | 16.06 | 0.92 | 0.22 | 0.22 | PC1 = 0.50, Prey = 0.22 |
| 3.0 km | $B_0 + B_1\text{PC1}^{\dagger}$ | -4.45 | 3 | 15.74 | 0.00 | 0.35 | 0.20 | |
| 3.0 km | $B_0 + B_1\text{PC1}^{\dagger} + B_2\text{Prey}$ | -3.72 | 4 | 16.88 | 1.14 | 0.20 | 0.21 | PC1 = 0.48, Prey = 0.21 |
| 3.5 km | $B_0 + B_1\text{PC1}^{\dagger}$ | -4.66 | 3 | 16.16 | 0.00 | 0.34 | 0.19 | |
| 3.5 km | $B_0 + B_1\text{PC1}^{\dagger} + B_2\text{Prey}$ | -3.94 | 4 | 17.32 | 1.16 | 0.19 | 0.19 | PC1 = 0.47, Prey = 0.21 |

[1] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] $^{\dagger}$Indicates a variable was significant at $P < 0.05$, $^{\dagger\dagger}$ indicates $P < 0.01$

Table 5.5. Summary of model selection statistics for evaluating the abundance of native Coccinellidae. The first model listed at each spatial scale is the minimum AICc model, bold indicates the best overall model. Only models with a $\Delta_i$ of 2 or less are included as competing models.

| Radius (km) | Model[1 2 3] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 1.0 km | $B_0 + B_1(\text{Year})^\dagger$ | 2.90 | 3 | 1.04 | 0.00 | 0.34 | 0.18 | |
| 1.5 km | $B_0 + B_1(\text{Year})^\dagger$ | 2.90 | 3 | 1.04 | 0.00 | 0.21 | 0.18 | |
| 1.5 km | $B_0 + B_1(\text{D})^\dagger$ | 2.58 | 3 | 1.68 | 0.64 | 0.15 | 0.16 | |
| 1.5 km | $B_0 + B_1(\text{D})^\dagger + B_2\text{PC2}$ | 3.47 | 4 | 2.50 | 1.46 | 0.10 | 0.18 | D = -0.42, PC2 = 0.34 |
| **2.0 km** | $\mathbf{B_0 + B_1(D)^\dagger + B_2PC2^\dagger}$ | **5.11** | **4** | **-0.78** | **0.00** | **0.21** | **0.26** | **D= -0.36, PC2= 0.37** |
| 2.0 km | $B_0 + B_1(\text{D}) + B_2\text{PC2}^\dagger + B_3(\text{Exotic})$ | 5.61 | 5 | 0.98 | 1.76 | 0.09 | 0.25 | D = -0.32, PC2 = 0.38, Exotic = -0.17 |
| 2.0 km | $B_0 + B_1(\text{Year})^\dagger$ | 2.90 | 3 | 1.04 | 1.82 | 0.09 | 0.18 | |
| 2.0 km | $B_0 + B_1\text{PC2}^\dagger$ | 2.81 | 3 | 1.22 | 2.00 | 0.08 | 0.17 | |
| 2.5 km | $B_0 + B_1(\text{D})^\dagger + B_2\text{PC2}^\dagger$ | 4.92 | 4 | -0.40 | 0.00 | 0.20 | 0.25 | D = -0.35, PC2 = 0.37 |
| 2.5 km | $B_0 + B_1(\text{Year})^\dagger$ | 2.90 | 3 | 1.04 | 1.44 | 0.10 | 0.18 | |
| 2.5 km | $B_0 + B_1\text{PC2}^\dagger$ | 2.76 | 3 | 1.32 | 1.72 | 0.09 | 0.17 | |
| 2.5 km | $B_0 + B_1(\text{D}) + B_2\text{PC2}^\dagger + B_3(\text{Exotic})$ | 5.37 | 5 | 1.46 | 1.86 | 0.08 | 0.24 | D = -0.32, PC2 = 0.38, Exotic = -0.16 |

Table 5.5 (continued)

| Radius (km) | Model[1 2 3] | Log-likelihood | $K_i$ | AICc | $\Delta_i$ | $W_i$ | Adjusted $r^2$ | Partial Correlations |
|---|---|---|---|---|---|---|---|---|
| 3.0 km | $B_0 + B_1(\text{D}) + B_2\text{PC2}^{\dagger}$ | 4.77 | 4 | -0.10 | 0.00 | 0.17 | 0.24 | D = -0.30, PC2 = 0.40 |
| 3.0 km | $B_0 + B_1\text{PC2}^{\dagger}$ | 3.21 | 3 | 0.42 | 0.52 | 0.13 | 0.19 | |
| 3.0 km | $B_0 + B_1(\text{Year})^{\dagger}$ | 2.90 | 3 | 1.04 | 1.14 | 0.10 | 0.18 | |
| 3.0 km | $B_0 + B_1\text{PC2}^{\dagger} + B_2(\text{Exotic})$ | 3.92 | 4 | 1.60 | 1.70 | 0.07 | 0.20 | PC2 = 0.46, Exotic = -0.20 |
| 3.0 km | $B_0 + B_1(\text{D}) + B_2\text{PC2}^{\dagger} + B_3(\text{Exotic})$ | 5.24 | 5 | 1.72 | 1.82 | 0.07 | 0.24 | D = -0.28, PC2 = 0.40, Exotic = -0.17 |
| 3.0 km | $B_0 + B_1(\text{PC1}) + B_2\text{PC2}^{\dagger}$ | 3.85 | 4 | 1.74 | 1.84 | 0.07 | 0.20 | PC1 = -0.19, PC2 = 0.47 |
| 3.5 km | $B_0 + B_1(\text{D}) + B_2\text{PC2}^{\dagger}$ | 5.09 | 4 | -0.74 | 0.00 | 0.17 | 0.25 | D = -0.28, PC2 = 0.44 |
| 3.5 km | $B_0 + B_1\text{PC2}^{\dagger\dagger}$ | 3.77 | 3 | -0.70 | 0.04 | 0.17 | 0.22 | |
| 3.5 km | $B_0 + B_1(\text{PC1}) + B_2\text{PC2}^{\dagger\dagger}$ | 4.45 | 4 | 0.54 | 1.28 | 0.09 | 0.23 | PC1 = -0.20, PC2 = 0.50 |
| 3.5 km | $B_0 + B_1\text{PC2}^{\dagger\dagger} + B_2(\text{Exotic})$ | 4.34 | 4 | 0.76 | 1.50 | 0.08 | 0.22 | PC2 = 0.49, Exotic = -0.18 |
| 3.5 km | $B_0 + B_1(\text{Year})^{\dagger}$ | 2.90 | 3 | 1.04 | 1.78 | 0.07 | 0.18 | |
| 3.5 km | $B_0 + B_1(\text{D}) + B_2\text{PC2}^{\dagger} + B_3(\text{Exotic})$ | 5.53 | 5 | 1.14 | 1.88 | 0.07 | 0.25 | D = -0.26, PC2 = 0.43, Exotic = -0.16 |

[1] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] $^{\dagger}$Indicates a variable was significant at $P < 0.05$, $^{\dagger\dagger}$ indicates $P < 0.01$

[3] Variables in parentheses indicate a negative relationship with native Coccinellidae abundance

Figure 5.1.

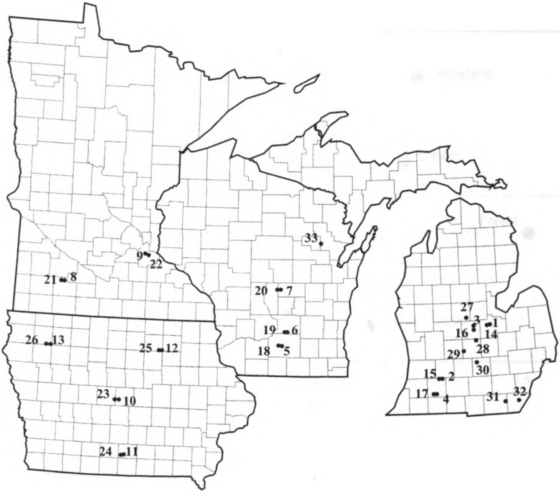


Figure 5.1. Location of 33 soybean fields sampled for coccinellids in 2005 (fields 1-13) and 2006 (fields 14-33) in Iowa, Michigan, Minnesota, and Iowa. Sites were selected so that the 3.5 km landscape radius surrounding each field varied in diversity and the abundance of natural and agricultural habitat.

Figure 5.2.

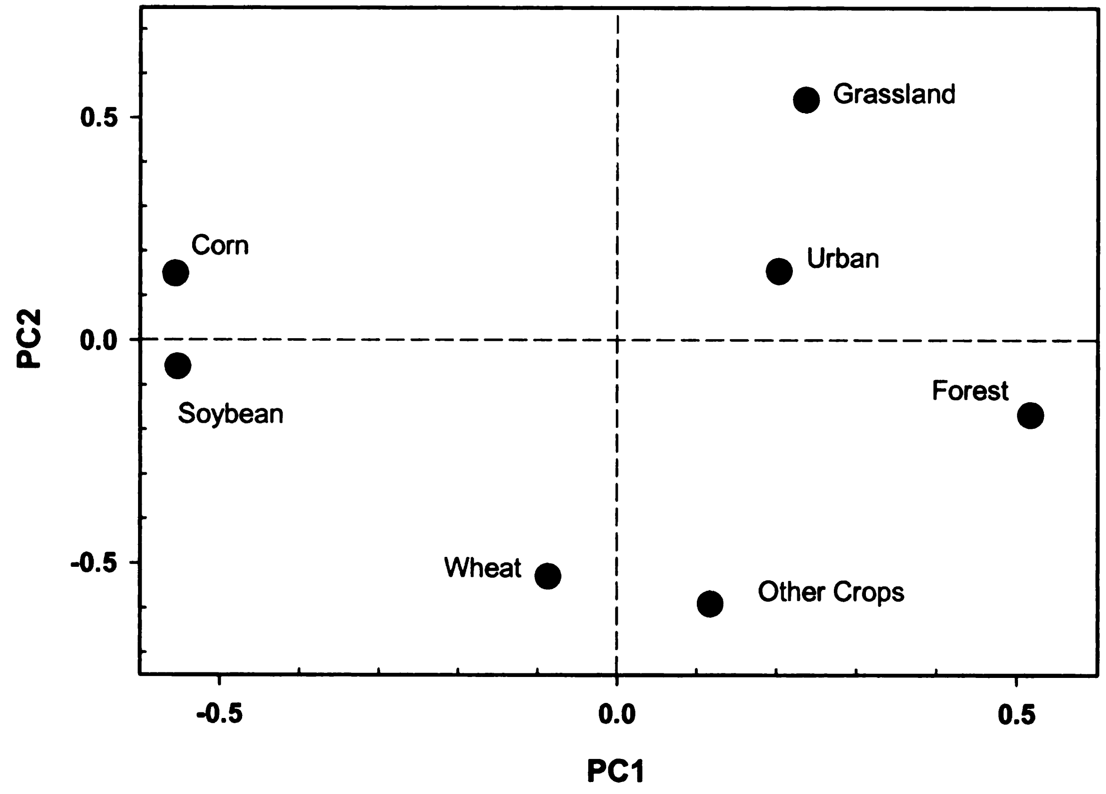


Figure 5.2. PCA ordination for principal components 1 and 2 of landscape elements surrounding soybean fields sampled at a radius of 1.5 km. Points indicate the principal component loadings of each variables included in the PCA analysis. Sites with positive loadings on PC1 were correlated with the variable Forest while negatives loadings on PC1 were correlated with the variables Corn and Soybean. Sites with positive loadings on PC2 were correlated with the variable Grassland while negative loadings on PC2 were correlated with the variables Other Crops and Wheat.

Figure 5.3.

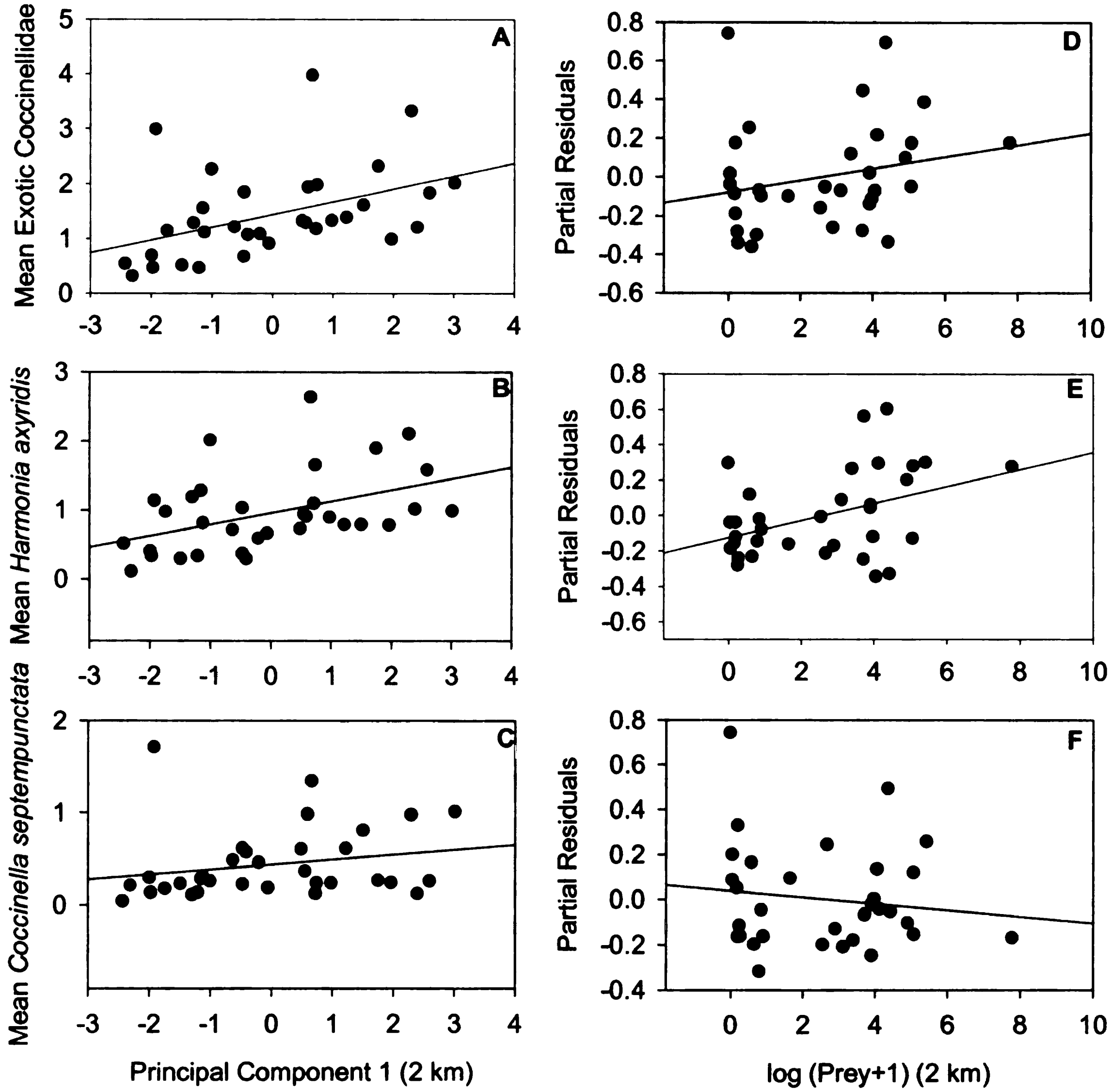


Figure 5.3. Relationship between the mean weekly catch of all exotic Coccinellidae (A), *H. axyridis* (B) and *C. septempunctata* (C) from yellow sticky card traps and the overall best fit model, PC1 at 2 km. Partial residual plots illustrate the relationship between the mean number of all exotic Coccinellidae (D), *H. axyridis* (E) and *C. septempunctata* (F) and soybean aphid abundance in the competing model, PC1+Prey at 2 km. Models were compared using an AIC$_c$ model selection procedure. Raw data means are shown in A-C, data were log (x+1) transformed for analysis.

Figure 5.4.

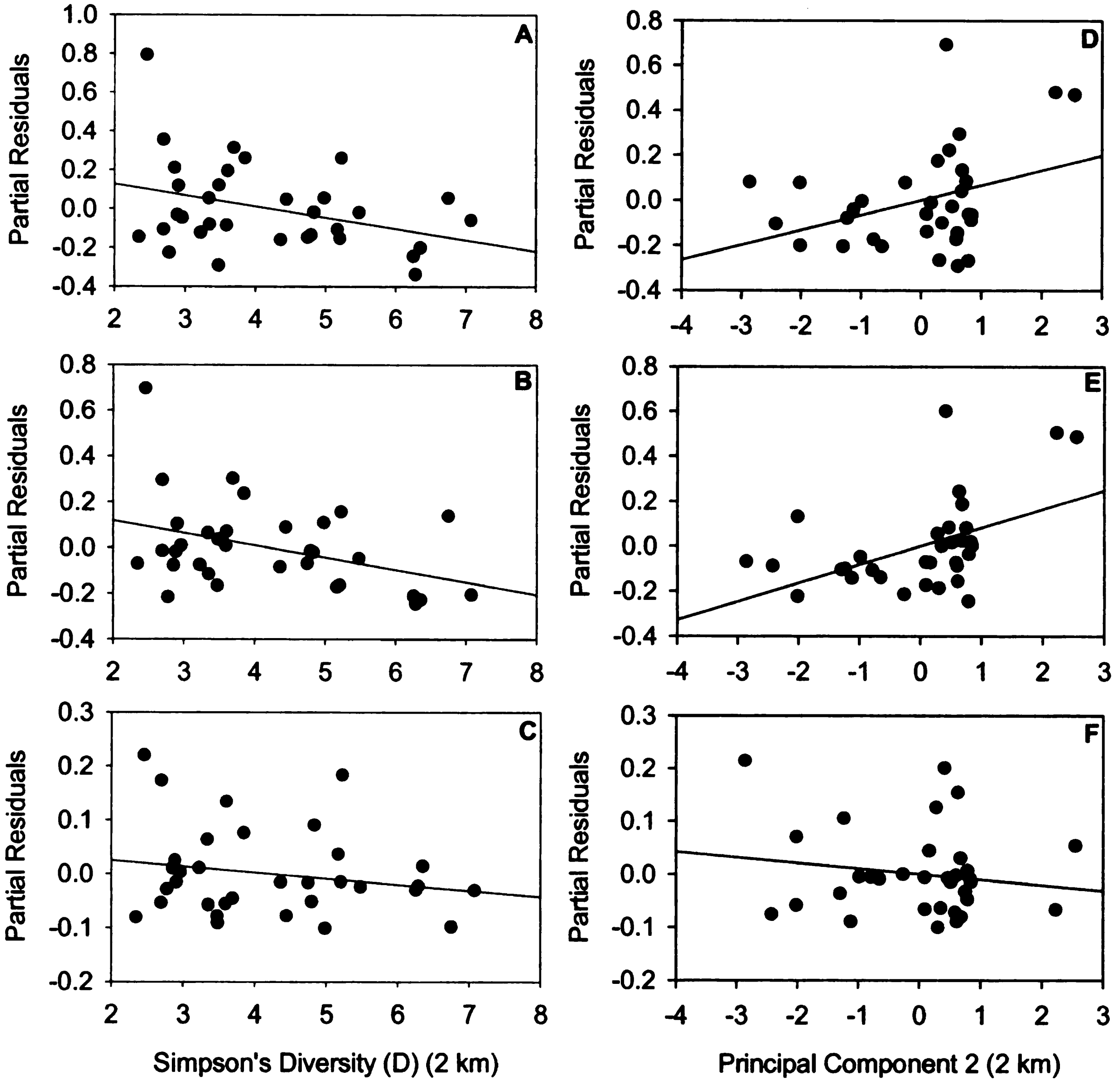


Figure 5.4. Partial residual plots illustrate the relationship between the mean weekly Catch of all native Coccinellidae (A and D), *H. convergens* (B and E), and *C. maculata* (C and F) from yellow sticky card traps and the best fit model Diverstiy+PC2 at 2 km determined using an AICc model selection procedure.

# CHAPTER 6

# NATIVE COCCINELLIDAE ARE SUBJECT TO SIGNIFICANT EGG PREDATION IN SOYBEAN FIELDS.

## Abstract

Intraguild predation (IGP) is a major factor shaping predator communities. Assemblages of predatory coccinellids are frequently important in suppressing herbivores in agroecosystems. However, in the past several decades, coccinellid communities across North America have been invaded by exotic coccinellids resulting in dramatic declines in some native species. I used the coccinellid community attacking soybean aphid in soybean in the north-central U.S. to test the hypotheses that IGP by exotic competitors is a major factor shaping native predator communities across differing agricultural landscapes. Previous studies have shown that coccinellid communities vary across the region and are related to the composition of the landscape surrounding soybean fields. My objectives were 1) to determine if observations of reduced native coccinellid abundance in Michigan were explained by greater IGP by exotic species and 2) to ascertain whether the area of forested patches across the study region was related to the amount of IGP incurred by native coccinellids. I measured the intensity of native coccinellid IGP in soybean fields in Michigan and Iowa using *Coleomegilla maculata* as a sentinel species and found that IGP occurred in 43% of eggs exposed to predators within 48 h. The majority of this predation is attributable to diurnally active predators. The intensity of *C. maculata* egg predation was consistent across both states; however, the composition of the potential egg predators varied. In Michigan, the exotic

coccinellids *C. septempunctata* and *H. axyridis* were the most abundant predators whereas in Iowa, the majority of those found were native species including *C. maculata*, *Hippodamia parenthesis* and the soft-winged flower beetle *Collops nigriceps*. Thus, in Michigan landscapes, consumption of native coccinellid eggs favors exotic coccinellids whereas in Iowa, this resource is more likely to sustain other native species. This study illustrates that it is not egg IGP *per se* but rather the overall composition of the IGP community in soybean that is contributing to the reduced native coccinellid community in Michigan versus Iowa.

## Introduction

Following successful 1889 introduction of the vedalia beetle, *Rodolia cardinalis* (Mulsant) into the U.S., over 100 species of exotic lady beetles have been either intentionally or accidentally released into North America (Harmon et al. 2007). Although many have either not established or are present at low densities, a few have become extremely abundant in agricultural habitats. In the north-central U.S., the two most prevalent species are *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas. Although these exotic coccinellid species can be beneficial in the control of several agricultural pests (Brewer and Elliott 2004, Snyder et al. 2004b, Costamagna and Landis 2007a, Gardiner et al. *in press*), increasing evidence suggests that their presence has resulted in the displacement of native coccinellid species (Putnam 1955, Wheeler and Hoebeke 1995, Elliott et al. 1996, Colunga-Garcia and Gage 1998, Michaud 2002, Snyder et al. 2004a, Harmon et al. 2007, Gardiner et al. *in press*). Understanding the factors that structure coccinellid communities is an important topic of both biological control and conservation science.

Both *C. septempunctata* and *H. axyridis* were originally introduced into the U.S. for biological control; however, it remains unclear whether their eventual establishment is due to intentional or accidental introductions (Schaefer et al. 1987, Day et al. 1994). *Coccinella septempunctata* was first detected in the U.S. in 1973; *H. axyridis* was detected 15 years later in 1988 (Schaefer et al. 1987, Chapin and Brou 1991). Recently, two additional exotic coccinellids, *Propylea quatuordecimpunctata* (L.) (Gardiner et al. *in review*) and *Hippodamia variegata* (Goeze) (Gardiner and Parsons 2005) have been detected in agricultural fields in the north-central U.S.

Over the last three decades, the food webs of native coccinellid species have undergone significant restructuring. Not only have additional competitors been added, but new prey species have also been introduced, including the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) and the soybean aphid, *Aphis glycines* Matsumura. Exotic coccinellids have been shown to be important predators of these exotic pests, and in turn the presence of these prey may have allowed exotic species to increase in abundance and expand their ranges.

The success of exotic coccinellids has been correlated with a decline in several native coccinellids in the U.S. One of the most dramatic declines is that of *Coccinella novemnotata* Herbst (Wheeler and Hoebeke 1995). Once common in the northeast, only 10 specimens have been collected in North America in the last 10 years (Losey et al. 2007). Wheeler and Hoebeke (1995) attribute this loss to the introduction of *C. septempunctata*. A similar pattern was documented in South Dakota by Elliott et al. (1996) who observed a 20-fold reduction in populations of *Coccinella transversoguttata richardsoni* Brown and *Adalia bipunctata* (L.) following the establishment of *C.*

*septempunctata*. With the establishment of *H. axyridis* came additional reports of native coccinellid decline. Colunga-Garcia and Gage (1998) reported a decrease in populations of *Brachiacantha ursina* (F.), *Cycloneda munda* (Say), and *Chilocorus stigma* (Say) in Michigan. More recently, Gardiner et al. (*in review*) failed to detect *Hippodamia convergens* Guérin-Méneville across two years of season-long sampling in Michigan, despite it being collected by previous investigators in recent years (Fox et al. 2005, Costamagna and Landis 2007a).

Gardiner et al. (*in review*) measured coccinellid diversity and abundance in soybean fields across Iowa, Michigan, Minnesota, and Wisconsin and found that the abundance of native species varied significantly across this region, from a low of 10% natives in Michigan to 44.8% natives in Iowa. They also found that the structure of the coccinellid community was tied to the composition of the landscape surrounding soybean fields. Landscapes with an abundance of forested habitat had the greatest proportion of exotic coccinellids while landscapes with an abundance of grasslands supported higher populations of native species.

Several studies have attributed native coccinellid decline to IGP by exotic species. While the propensity of exotic coccinellids to act as intraguild predators has been well documented (Cottrell 2004, Snyder et al. 2004a, Cottrell 2005, 2007, Gardiner and Landis 2007) the intensity of egg predation experienced by native coccinellids had not been measured at a regional scale. My goal was to determine if the pattern of native coccinellid abundance in Michigan and Iowa illustrated by Gardiner et al (*in review*) was explained by differences in the extent of egg predation incurred by native coccinellid populations in these states. My hypotheses were that 1) egg predation would be greater in Michigan soybean fields due to a greater abundance of exotic coccinellids compared with Iowa and 2) landscapes with extensive forested habitat within both states would support greater egg predation than grassland or cropland dominated landscapes.

## Methods

### *Field sites*

During July of 2007, I measured the intensity of predation on sentinel egg masses of C. *maculata* in n=14 soybean fields in Michigan (n=8) and Iowa (n=6) (Figure 6.1). A minimum distance of 10 km separated each field site. Field size averaged 12.5 ha (range: 3.0-60.4 ha). Within each state, soybean fields were located within landscapes which ranged from very simple landscapes comprised primarily of cropland to complex landscapes with an abundance of natural habitats. Within each soybean field, four 0.2 ha plots were established where all sampling took place. Soybean fields were not treated with insecticide during the study period.

### *Egg mass collection*

Beginning in May 2007, *C. maculata* adults were field collected from grasslands and alfalfa fields in Iowa using sweep nets. Females were placed individually into Petri dishes with strips of paper to serve as an egg-laying substrate. Beetles were provided daily with water, honey and eggs of the corn earworm, *Helicoverpa zea*. Dishes were checked daily for *C. maculata* eggs and any found were frozen (- 80 ˚C). I determined that 15 eggs per mass was the average size deposited by *C. maculata* under these conditions and therefore used egg masses of this size in the field experiment. To prepare sentinel egg masses, individual eggs were either added or removed from existing masses using a paint brush, to reach n=15 eggs per strip. Added eggs were attached to the paper strip using water soluable glue (Elmer's Products, Columbus, OH). The standardized egg masses were cut out and glued onto filter paper disks (12 mm diameter). Egg masses remained frozen until they were transported to the field.

### *Measuring predation of frozen egg masses*

Prior to field experiments, I compared predation of previously frozen and live *C. maculata* eggs by four commonly found intraguild predators: *C. septempunctata*, *H. axyridis*, *H. parenthesis* and *Nabis* sp. Individual predators were released into a Petri dish arena containing three thawed and three fresh eggs, randomly arranged in a grid pattern. All arenas were checked hourly for 8 h then again at 18 and 24 h and the number and type of eggs consumed by each predator were recorded. Ten replicates were completed for each predator species. None of the species tested showed significant preference for either thawed or live eggs (24 h: *C. septempunctata* $P$=0.4595, *H. axyridis* $P$=1.000, *H. parenthesis* $P$=0.6132, *Nabis* sp. $P$=0.1480).

### *Egg predation experiment*

To begin the experiment, two filter paper disks containing egg masses were glued onto the top side of a soybean trifoliate leaf approximately 15 cm from ground level on adjacent plants in the center of each plot. The exclusion egg treatment consisted of one egg mass enclosed in a 22 cm clip cage to prevent predators from accessing the eggs. The open egg treatment consisted of an un-caged egg mass open to predation. Both treatments remained in the field for 48 h after which they were collected and examined to determine the number of undamaged eggs remaining. After 48 h of exposure in the field 40% of eggs in the caged treatment were partially collapsed, mimicking damage that could be caused by piercing sucking predators. To eliminate potential confusion I only considered eggs to be predated-upon if there was clear evidence of damage from a chewing predator. Thus, my measure of egg predation does not account for losses due to piercing sucking predators and is thus likely to be conservative compared with the field reality.

### *Nocturnal egg predation experiment*

To account for what proportion of egg predation was due to nocturnally active predators, I conducted a nocturnal predation experiment in eight sites (four per state). Open and caged egg mass treatments were placed within the center of each plot on adjacent plants at dusk 2000-2200 h and removed at dawn 0500-0700 h and the number of undamaged eggs recorded.

### *Predator and soybean aphid survey*

During the 48 h egg predation experiment, I measured the activity of potential egg predators by placing one unbaited yellow sticky card (PHEROCON AM, Great Lakes IPM, Vestaburg, MI) in the center of each plot. A metal "T" fence post was erected and a 22.9 x 27.9 cm sticky card was suspended just above the plant canopy. Sticky traps remained in the field for 48 h. All potential egg predators were counted and identified to species. I also measured the abundance of predators by collecting a 20-sweep sample from two rows of soybean plants in each plot. As the abundance of prey may effect the intensity of egg predation, I also measured soybean aphid populations within each field site using destructive plant counts. In each plot, five randomly selected plants were removed from the ground and the number of apterous and alate *A. glycines* were counted on each plant.

*Landscape analysis*

Field geospatial data were collected using a handheld GPS receiver using Wide Area Augmentation System (WAAS) correction. The spatial coordinate (WSG 1984) for the center of each site was used to obtain ortho-rectified digital aerial imagery for the site. I digitized the habitats surrounding each study site to a radius of two km using ARC GIS 9.1 and conducted ground verification of each landscape from July-August 2007. Each landscape polygon within two km of the center of the study sites was given a value corresponding to one of seven landscape categories: corn, soybean, other crops, forest, grassland, wetland and open water, and urban. Some locations included polygons that were not visible from a roadway and permission to access private lands could not be obtained. These polygons were given a value of zero and were excluded from further analysis. The area of each site that could not be identified was very low (<1%). The smallest polygons identified included field plots on university research farms and small patches of abandoned crop field ($< 5\ m^2$) the largest were contiguous forests, grasslands and crop fields ($\leq 1.3\ km^2$).

Landscape diversity was measured using Simpson's Index (D) (Simpson 1949). Simpson’s Index is typically used to examine the variance of species abundance distributions, here I applied it to examine variance in the proportion of area covered by each of seven land cover categories. The equation for Simpson’s Index (D) is: $D = 1/\sum(p_i)^2$ where $p_i$=proportion of habitat in the $i^{th}$ land-cover category (D increases as diversity increases).

*Statistical analysis*

For both egg predation experiments, a split-plot mixed effects analysis of variance model (ANOVA) was used to determine if a significant number of *C. maculata* eggs were removed by predators. This model included Treatment and State as fixed effects and a State by Treatment interaction. Random effects were Site nested within State and Plot nested within Site and State.

A log likelihood chi-square test assuming a multinomial distribution was used to examine the variation in the community of potential egg predators in Michigan and Iowa soybean fields (Shao 2003). This test determines if the species composition of the coccinellid community within each state is significantly different. The null hypothesis for this test was that the proportional distribution of predator species within Michigan and Iowa did not differ. This test was completed using compiled species data from sticky cards and sweep net samples. Both the ANOVA models and log likelihood chi-square test were completed using SAS v. 9.1 (SAS Institute 1999).

To asses the influence of landscape on the intensity of egg predation, four models were compared using Akaike's Information Criterion, adjusted for a small sample size (AICc) (Burnham and Anderson 2002). These included an intercept only model and models containing the variables; proportion forested habitat, proportion grassland habitat, overall landscape diversity (Simpson's D) and extraguild prey abundance (Table 6.1). The maximum log-likelihood estimate, the Akaike weights (estimate the relative likelihood of a given model against all other models) and AICc differences ($\Delta_i$) are presented. The model with the minimum AICc value is considered to have the best support for the data. Any model with a $\Delta_i$ of less than two is termed a "competing model" (Ribic and Sample 2001) and is also considered to also have substantial support for the data (Burnham and Anderson 2002). Once the minimum AICc and competing models were determined, I also examined the relationship between these models and the average number of potential egg predators collected per 20-sweep sample in soybean fields. For each model I calculated the $r^2$ to evaluate how well the models explained the variation in the data. The AICc analysis was conducted using R version 2.1.1 (R Development Core Team 2005). The average number of predators per 20-sweep sample was log (x+1) transformed prior to analysis.

## Results

### *Egg predation experiment*

Egg masses of *C. maculata* were subject to significant intraguild predation in soybean fields across Michigan and Iowa after 48 h of field exposure ($F_{1,54}$=45.73, *P*<0.001) (Figure 6.2). In the open treatment, 43% of the *C. maculata* eggs were removed. Predation events were recorded on 60.7% of egg masses, with an average of 4.4 eggs remaining after 48 h. There was no significant difference in the amount of predation incurred between the states (State*Treatment interaction: $F_{1,54}$=3.18, *P*=0.0804).

### *Nocturnal egg predation experiment*

Predators removed 6.2% of the available eggs during the nocturnal predation experiment (experiment run for 9 h, 2000-2200 h to 0500-0700 h). There was no significant difference between the number of eggs remaining in caged and open treatments ($F_{1,30}$=1.83, *P*=0.1725) (Figure 6.2). After exposure, the average number of eggs remaining in open egg masses was 13.9 ± 0.6 compared with 14.8 ± 0.1 in the caged treatment.

### *Aphid and predator populations*

Aphid populations in soybean fields during the egg experiment were low across the 14 sites, varying from 0 per plant (Monroe and Britton MI) to 21.4 ± 4.5 per plant (Ames, IA). In both states, low numbers of chewing predators were detected averaging 0.3 ± 0.1 and 0.7 ± 0.1 per 20 sweeps in Iowa and Michigan respectively (Table 6.2). Chewing predators on yellow sticky cards averaged 0 per card in Iowa and 1.6 ± 0.2 in Michigan. Six species of potential egg predators were collected: *H. axyridis*, *C. septempunctata*, *P. quatuordecimpunctata*, *C. maculata*, *H. parenthesis* and the soft-winged flower beetle *Collops nigriceps* (Say) (Melyridae) (Table 6.2). The species composition of these communities in Michigan and Iowa soybean fields were significantly different ($X^2_5$=28.28, P<0.0001) (Table 6.2). In Michigan, the community was dominated by the coccinellids *H. axyridis* and *C. septempunctata*. In Iowa, *C. nigriceps* comprised 50% of the predator community followed by *C. maculata*, *H. parenthesis* and *H. axyridis* which each accounted for 16.7%. As C. *nigriceps* was not included in preliminary testing, I subsequently measured its potential as a predator of *C. maculata*. Four specimens were placed into individual Petri dishes each with a thawed *C. maculata* egg mass. Within 3 h, 3 of 4 *C. nigriceps* consumed all 15 eggs, in the fourth replicate the beetle did not consume any eggs after 24 h.

### *Landscape diversity*

Within the 2 km landscape radius surrounding each of the 14 sites, landscape diversity values (Simpson's D) ranged from 2.12-5.31. The percentage of the landscape composed of cropland ranged from 15-86%. Landscapes with high and low percentages of cropland occurred in both Michigan 18-95% and Iowa 23-88%. Forested habitat comprised from 0.04-22% of the landscape in Iowa sites and 2-21% of Michigan landscapes.

### *AICc analysis of egg predation and landscape variables*

The diversity model predicting the abundance of eggs after 48 h had the lowest AICc value (Table 6.3). There was a marginally significant ($P = 0.0774$) negative relationship between D and the number of eggs removed in the open treatment after 48 h (Figure 3). This indicates that the intensity of egg predation in soybean fields is slightly higher in simple, agriculturally-dominated landscapes compared to diverse landscapes with an abundance of non-crop habitat. The intercept model was a competing model with a $\Delta_i$ of 1.33, indicating the intercept alone provides nearly equal support to the data compared with the predictor Simpson's D (Table 6.3). Predator abundance in fields was positively correlated with Simpson's D, the average number of predators found in 20-sweep samples was greater in diverse landscapes with an abundance of forests and grasslands.

## Discussion

Over the last 20 years several studies have documented declines in native Coccinellidae populations in the U.S. Many have attributed this to predation of native eggs and larvae by exotic coccinellid species, primarily *H. axyridis* and *C. septempunctata*. In this study, I measured the intensity of intraguild predation of native coccinellid eggs within soybean fields in two states that vary in the structure of the coccinellid community. Michigan communities were composed of 10% native species versus 44.8% native species in Iowa (Gardiner et al. *in review*). This difference has been linked to the composition of the landscape surrounding soybean fields, with landscapes dominated by grasslands supporting higher native coccinellid populations while forested landscapes support a greater abundance of exotics. My hypothesis was that the reduced amounts of forest habitats in Iowa would limit the success of exotic coccinellids and thus the intensity of IGP, leading to a greater abundance of native species. In contrast, I found significant native coccinellid egg predation in soybean fields throughout both Michigan and Iowa. Although the extent of egg predation detected was consistent across the states studied, the guild of egg predators exploiting this resource varied. The community of egg predators in Michigan was dominated by the exotic coccinellid species whereas the Iowa community was comprised primarily of native predators.

### *Egg predation of C. maculata*

This study illustrates that the intensity of *C. maculata* egg predation in soybean fields is high, with predators consuming 43% of available eggs within 48 h. This is the first account of egg predation of a native coccinellid, illustrating that egg predation likely plays a significant role in its population dynamics. However, depending on the landscape context of any given field, the community of predators consuming native coccinellid eggs will vary. Since exotic species were the most abundant coccinellids collected from Michigan soybean fields both in this study and previous studies (Gardiner et al. *in review*) they are likely to have contributed significantly to the predation of *C. maculata* eggs. Both laboratory studies and field observations illustrate that *H. axyridis* and *C. septempunctata* larvae and adults are significant predators of native coccinellid eggs and larvae (Cottrell 2004, Snyder et al. 2004a, Cottrell 2005). These exotic species are more likely to act as intraguild predators of native species, rather than intraguild prey (Cottrell 2004, Snyder et al. 2004a, Cottrell 2005, Yasuda 2006). In addition, *H. axyridis* is able to complete its development on a diet of native coccinellid eggs, while native coccinellid larvae cannot reach adulthood on a diet of *H. axyridis* eggs (Cottrell 2004). The presence of *H. axyridis* has also been found to result in interference competition with heterospecifics, resulting in reduced fecundity in native species (Soares and Serpa 2007).

Whereas exotic coccinellids were the most abundant predators in Michigan soybean fields, the potential egg predator community in Iowa was composed primarily of native species. Although it is likely that exotic species play a significant role in the intraguild predation of native coccinellid eggs throughout their invaded range, it is likely that native species also consume coccinellid eggs. Several native coccinellids are known to consume the eggs of other coccinellids as well as conspecifics (Cottrell and Yeargan 1998a, b). I also determined that the melyrid *C. nigriceps* found in Iowa soybean fields fed on *C. maculata* eggs.

*Contribution of nocturnal egg predators*

To accurately identify predation pressure on a specific prey, it is critical to account for activity of both diurnal and nocturnal natural enemy species (Pfannenstiel and Yeargan 2002). I found that 6.2% of eggs exposed to nocturnal predators were preyed upon in a single night. Assuming equal predation for both nights of the study, I estimate that 12.5% of available eggs in the 48 h egg predation study were consumed at night, or approximately 30% of the total eggs consumed. Other studies in soybean have also found significant nocturnal predation. Pfannenstiel and Yeargan (2002) observed that *C. maculata* larvae, Phalangiidae, *Clubiona abbotii* (Clubionidae), Elateridae, Carabidae, and *Lygus lineolaris* (Lygeidae) were all nocturnally active predators of lepidoptern eggs in corn and soybean fields. As I only recorded damage from chewing predators, I did not account for potential predation by spiders, opiliones, or true bugs. Of the remaining chewing predators found by Pfannenstiel and Yeargan (2002), only *C. maculata* larvae are known to consume *C. maculata* eggs. Pfannenstiel and Yeargan (2002) report that *C. maculata* adults were diurnal feeders while larvae remained active at night.

### *Local landscape effects on C. maculata egg predation*

A marginally significant negative correlation was detected between landscape diversity (D) and the number of *C. maculata* eggs consumed within 48 h. At a spatial scale of 2 km, soybean fields in low diversity agricultural landscapes experienced greater *C. maculata* egg predation compared with high diversity landscapes with an abundance of non-crop habitat. My hypothesis was that egg predation would increase in soybean fields in diverse landscapes as these landscapes would supply a greater number of potential egg predators. Although potential egg predator abundance did increase with landscape diversity, egg predation declined. It is possible that the predator species found in simple, agricultural landscapes were more likely to consume native coccinellid eggs than those supplied by diverse landscapes. Alternatively, although the abundance of soybean aphid did not impact egg predation in soybean fields, diverse landscapes may have a greater abundance of total available prey, reducing the likelihood of egg predation in the open egg treatment in fields in these landscapes.

### *A new hypothesis for native coccinellid decline*

This study investigated one potential mechanism to explain the differences in coccinellid community composition found by Gardiner et al. (*in review*). I investigated the hypothesis that lower populations of exotic coccinellids in Iowa soybean fields would result in reduced intraguild egg predation of native coccinellids, sustaining native communities. However, the data support a different hypothesis for greater exotic dominance in Michigan compared with Iowa. I found that it was not the intensity of egg predation in soybean that varied, but the community of likely intraguild predators. I propose a landscape-mediated IGP hypothesis, where the abundance of a coccinellid species is driven by landscape structure and perpetuated by within-field interactions between guild members (Figure 6.4). For example, the abundance of exotic coccinellids in soybean fields is positively related to the amount of forested habitat within the landscape. Therefore, exotic species are likely to dominate coccinellid communities in soybean fields in forested landscapes. In these exotic-dominated food webs, native coccinellid eggs are likely to contribute to the maintenance of exotic populations. Alternatively, landscapes with an abundance of grassland habitat support higher populations of native coccinellids in soybean fields. In food webs with a greater proportion of native species, intraguild predation of coccinellid eggs is likely to benefit both native species and exotic competitors. Therefore, a greater proportion of the resources from native coccinellid eggs will build and sustain native food webs in grassland-dominant landscapes (Figure 6.4).

### *Summary*

Gardiner et al. *(in review)* were the first to illustrate that patterns in the abundance of native and exotic lady beetles are affected by landscape composition. Although Gardiner et al. (*in review*) demonstrated that native and exotic coccinellids populations in soybean fields are favored by different types of landscapes, it was unknown if competitive or predatory interactions between these species caused this partitioning. Two scenarios were discussed: 1) native species may be adapted to more open savanna and prairie landscapes that formerly dominated large areas of the north-central U.S. and thus still favor landscapes with an abundance of grassland habitat. However, this did not explain the relatively recent decline in native coccinellids within the last few decades, long after landscapes were transformed by human settlement. 2) Alternatively, it may be that these native species are still thriving in landscapes that are less favorable to invasion by exotic coccinellids, which act as strong intraguild predators. Since exotics are favored by forested habitat, a lack of these landscape elements may have restricted *H. axyridis* dominance of coccinellid communities in these areas favoring persistence of native coccinellid communities.

This study illustrates that it is not the intensity of IGP that is contributing to the decline in native coccinellids but more likely the structure of the predator guild consuming this resource. In landscapes that favor exotic coccinellids, native coccinellid eggs are more likely to be consumed by exotic predator guilds. This is likely contributing to the decline in several native coccinellid species in forested states such as Michigan were populations of *B. ursina*, *C. munda, C. stigma, and H. convergens* have noticeably declined (Colunga-Garcia and Gage 1998, Gardiner et al. *in review*). Alternatively, despite overall equal egg predation in Iowa, the presence of fewer exotic competitors is likely to favor the persistence of native coccinellid populations and could protect native biodiversity.

Although it may be impossible to remove established exotic coccinellids from the environment, we can protect native biodiversity by protecting and promoting landscape attributes which favor native coccinellid populations. Grasslands appear to be very important in supplying native coccinellids to soybean fields (Gardiner et al. *in review*) and thus should be a high conservation priority to preserve these species. Further, the majority of work on exotic and native coccinellids has focused on their populations in agricultural fields (Snyder and Evans 2006), which likely function as sink populations supplied by surrounding natural habitats. Future work must focus on understanding interactions between source populations of native and exotic coccinellids, in grassland and forested habitats.

Table 6.1. Five potential models to explain the intensity of egg predation in Michigan and Iowa soybean fields located in landscapes of varying diversity, abundance of forest and grassland habitats, and the availability of extraguild prey. The models were compared using AIC analysis adjusted for a small sample size (AICc). The *a priori* hypothesis for testing each model is also provided.

| Model | Hypothesis |
|---|---|
| **Intercept Model**<br>y = $B_o$ | Null Hypothesis: Landscape variables and prey abundance do not impact the amount of native coccinellid egg predation in soybean fields. |
| **Forest Model**<br>y = $B_o + B_1$Forest | Landscapes which support high populations of exotic coccinellids (high proportion of forest) in soybean fields will support greater native coccinellid egg predation |
| **Grassland Model**<br>y = $B_o + B_1$Grassland | Landscapes which support high populations of native coccinellids (high proportion of grassland) in soybean fields will support greater native coccinellid egg predation |
| **Diversity Model**<br>y = $B_o + B_1$Diversity[1] | Diverse landscapes are likely to include a greater abundance of non-crop habitats that supply native and exotic coccinellids to cropland. This will result in greater native coccinellid egg predation in soybean fields. |
| **Prey Model**<br>y = $B_o + B_1$Prey[2] | Soybean fields with a lower extraguild prey abundance will support greater native coccinellid egg predation |

[1] Diversity = Simpson's Diversity where D = $1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[2] Prey is the average number of soybean aphids per plant within each field site found during the 48 h egg predation study

Table 6.2. Percent of the total predator community and mean abundance ± SEM of predators found in Iowa and Michigan soybean fields using two sampling measures: sweep samples and yellow sticky card traps. Sweep samples consisted of a 20-sweep sample of two rows of soybean plants. Yellow sticky cards were placed just above the plant canopy and remained in the field for 48 h (during the 48 h egg predation experiment).

| | **Sweep Net** | | | |
|---|---|---|---|---|
| | Percentage of Total | | Mean ± SEM | |
| **Predator Species** | Iowa | Michigan | Iowa | Michigan |
| *H. axyridis* | 16.7 | 33.3 | 0.04 ± 0.04 | 0.22 ± 0.07 |
| *C. septempunctata* | 0.0 | 57.1 | 0 | 0.38 ± 0.11 |
| *P. quatuordecimpunctata* | 0.0 | 4.8 | 0 | 0.03 ± 0.03 |
| *C maculata* | 16.7 | 0.0 | 0.04 ± 0.04 | 0 |
| *H. parenthesis* | 16.7 | 4.8 | 0.04 ± 0.04 | 0.03 |
| *C. nigriceps* | 50.0 | 0.0 | 0.13 ± 0.09 | 0 |
| **Total** | 100 | 100 | 0.25 ± 0.12 | 0.66 ± 0.12 |

| | **Yellow Sticky Trap** | | | |
|---|---|---|---|---|
| | Percentage of Total | | Mean ± SEM | |
| | Iowa | Michigan | Iowa | Michigan |
| *H. axyridis* | 0 | 27.0 | 0 | 0.31 ± 0.09 |
| *C. septempunctata* | 0 | 70.3 | 0 | 0.81 ± 0.20 |
| *H. parenthesis* | 0 | 2.7 | 0 | 0.03 ± 0.03 |
| **Total** | 0 | 100 | 0 | 1.16 ± 0.20 |

Table 6.3. Summary of model selection statistics for evaluating the intensity of egg predation in soybean fields in Iowa and Michigan.

The minimum AICc model and competing models appear in bold.

| Model [1] | Log-likelihood | $K_i$ | AICc | $W_i$ | $\Delta_i$ | Adjusted $r^2$ |
|---|---|---|---|---|---|---|
| **y = $\boldsymbol{B_o + B_1}$(Diversity)**[2] | **-40.85** | **3** | **89.06** | **0.49** | **0.00** | **0.17** |
| **y = $\boldsymbol{B_o}$** | **-42.74** | **2** | **90.39** | **0.25** | **1.33** | |
| y = $B_o + B_1$(Forest)[3] | -42.54 | 3 | 92.44 | 0.09 | 3.38 | -0.05 |
| y = $B_o + B_1$(Grassland)[3] | -42.59 | 3 | 92.54 | 0.09 | 3.48 | -0.06 |
| y = $B_o + B_1$(Prey)[4] | -42.74 | 3 | 92.84 | 0.07 | 3.78 | -0.08 |

[1] Variables in parentheses indicate a negative relationship with egg predation

[2] D = Simpson's Diversity where $D = 1/\sum(pi)^2$ and pi=proportion of habitat in the ith land-cover category

[3] Forest = proportion of landscape with a 2 km radius surrounding soybean field composed of forested habitat, Grassland = proportion of landscape with a 2 km radius surrounding soybean field composed of grassland habitat, including pasturelands, restored prairies, and old fields.

[4] Prey = average abundance of soybean aphid, *Aphis glycines*, in soybean fields at the time of the 48 h egg predation experiment, measured using destructive plant counts.

Figure 6.1.

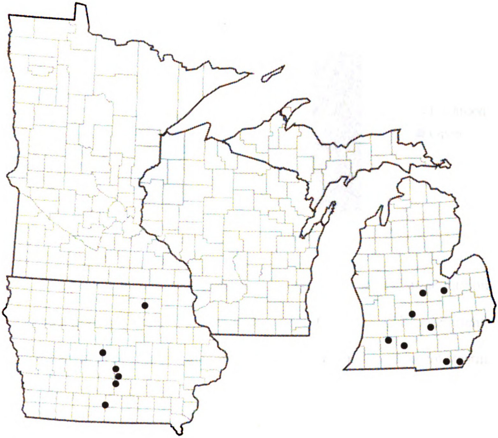


Figure 6.1. Location of 14 soybean fields in Michigan and Iowa where *C. maculata* egg predation was measured during July of 2007. The distance between each location was 10 km or greater. Sites were selected so that the 2 km landscapes surrounding each field varied in diversity and the abundance of natural and agricultural habitat within each state.

Figure 6.2.

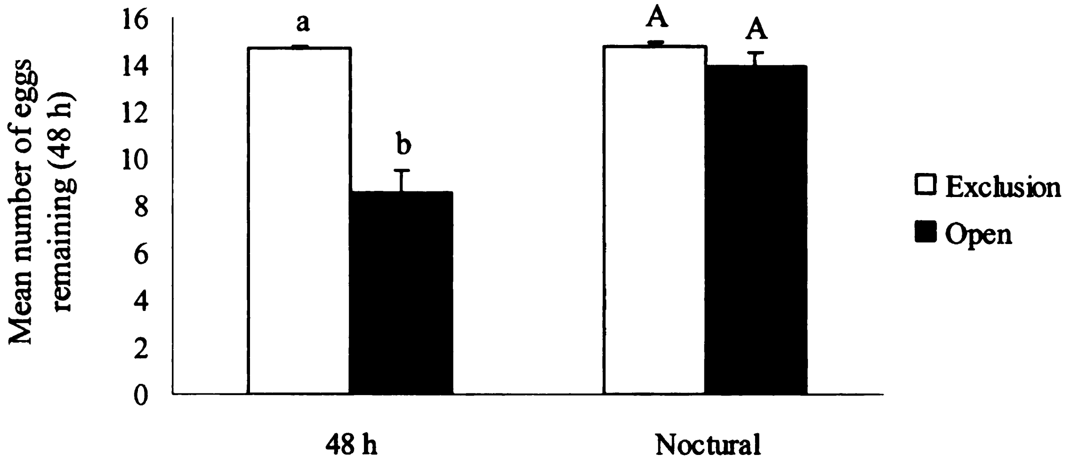


Figure 6.2. Mean number of eggs remaining in the exclusion cage treatment (white bars) and open treatment (black bars) in predation experiments. In the 48 h experiment, treatments remained in soybean fields for 48 h, while nocturnal experiment treatments remained in fields for 9 h.

Figure 6.3.

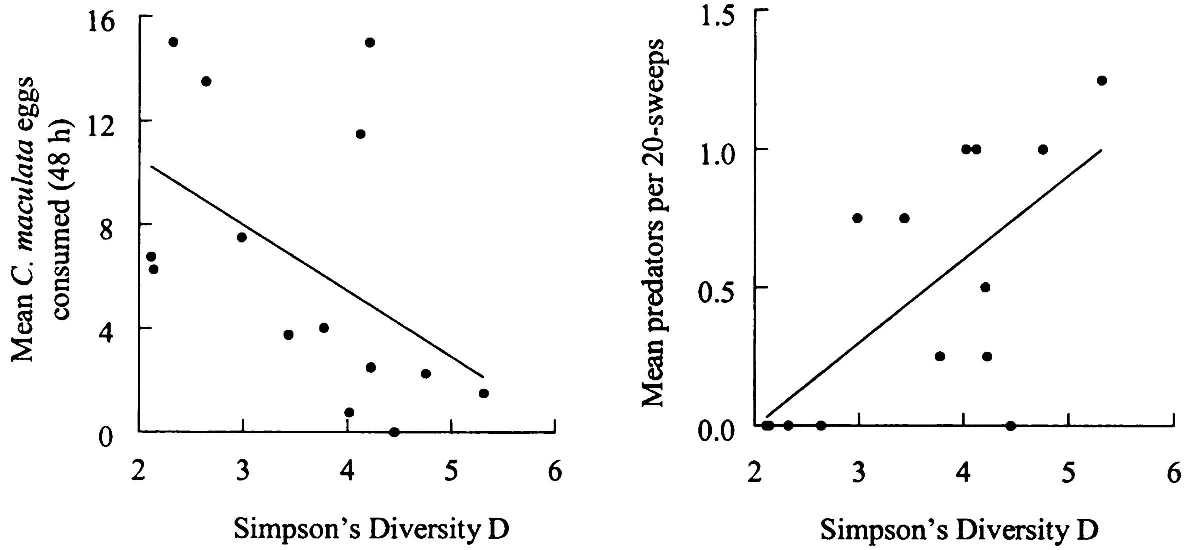
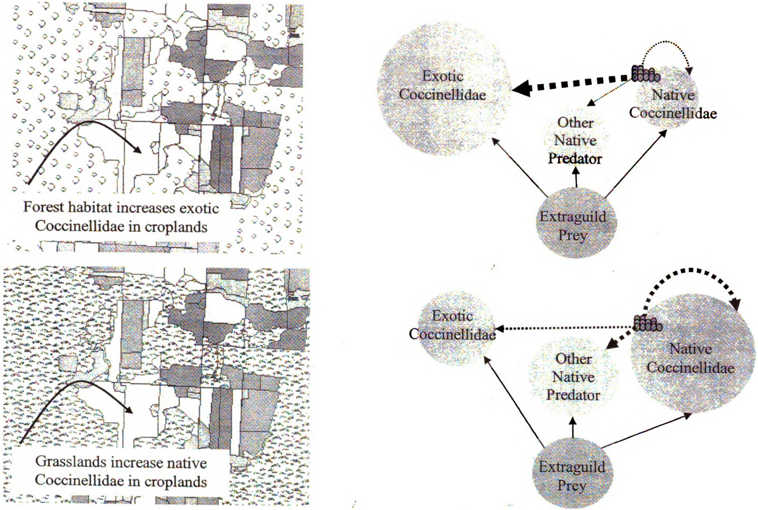


Figure 6.3. Relationships between landscape diversity (D), the number of *C. maculata* eggs consumed after 48 h of exposure to predators in soybean fields, and the average number of egg predators collected per 20-sweep sample of soybean foliage. Landscape diversity was estimated from 7 land-use categories using the Simpson's Diversity Index (D): $D = 1/\sum(p_i)^2$ where $p_i$=proportion of habitat in the $i^{th}$ land-cover category (D increases as diversity increases). The mean number of predators per 20-sweep sample was log (x+1) transformed prior to analysis. Untransformed means are shown here for interpretation.

Figure 6.4. The landscape-mediated IGP hypothesis. Gardiner et al. (*in review*) found that native and exotic coccinellid populations in soybean fields were associated with different landscape elements. Soybean fields in forested landscapes were dominated by exotic coccinellids (Michigan) while soybean fields in landscapes with an abundance of grassland (Iowa) had greater native coccinellid abundance. I propose that native coccinellid populations are under greater threat from exotics in soybean fields in forest dominated landscapes. Here, exotics are more likely to occupy a larger proportion of the guild of potential intraguild predators and thus consume a greater proportion of native coccinellid eggs. In grassland dominated landscapes native eggs are more likely to be utilized by native predators, sustaining their populations. In the above food web, circle size indicates the relative abundance of species within the food web. Solid lines indicate predator-prey interactions while dotted lines indicate potential IGP. Width of dotted lines indicates the proposed strength of intraguild interactions.

Figure 6.4.


Forest habitat increases exotic Coccinellidae in croplands
Exotic Coccinellidae
Other Native Predator
Native Coccinellidae
Extraguild Prey
Grasslands increase native Coccinellidae in croplands
Exotic Coccinellidae
Other Native Predator
Native Coccinellidae
Extraguild Prey

# CHAPTER 7

## CONCLUSIONS AND FUTURE DIRECTIONS

The soybean aphid, *Aphis glycines* Matumura, is an invasive species first detected in the U.S. in 2000. This pest has now spread throughout the north-central soybean growing states and Canadian provinces. Previous work has demonstrated that natural enemies are key drivers of soybean aphid population dynamics within soybean fields (Fox et al. 2004, Rutledge et al. 2004, Fox et al. 2005, Costamagna and Landis 2007a, Costamagna et al. 2007a, Costamagna et al. 2007b, Costamagna et al. *in press*). The objectives of my dissertation research were to investigate how landscape diversity and composition influenced the species pool of potential biocontrol agents supplied to soybean fields and determine how within-field interactions between these species impact biocontrol services. I investigated these objectives in replicate sites across Iowa, Michigan, Minnesota, and Wisconsin from 2005-2007.

Overall, I found that both landscape composition and within-field interactions affected the diversity, abundance, and biocontrol services provided by the predator community in soybean fields. The distribution and abundance of semi-natural and agricultural habitats within the landscape greatly influenced the abundance of key predator species including Coccinellidae, Carabidae, Araneae and Opiliones. While I expected all taxa to increase with landscape diversity and the amount of semi-natural habitat present, I found variation in the response of the study organisms based on their trophic level, phenology, and whether they were native to the north-central U.S. The activity density of Araneae increased in soybean fields in landscapes with an abundance of forests and grasslands. Relationships with Carabidae activity density varied, with adult overwintering and predatory species increasing and larval overwintering species declining with the abundance of grassland in the landscape. The coccinellid community also exhibited varied responses to landscape diversity and composition. I found that native coccinellids were most abundant in low-diversity landscapes with an abundance of grassland habitat whereas exotic coccinellid increased with the abundance of forested habitats. The biocontrol services supplied to soybean fields by these species is a function of landscape diversity, with diverse landscapes supplying greater biocontrol service compared with simple landscapes dominated by agricultural habitats.

My studies illustrated that landscape diversity and composition were key in supplying a species pool of predators to provide biocontrol services, and that within-field interactions that occurred between these species influenced their community dynamics. Exotic coccinellids acted as significant intraguild predators of native coccinellids, lacewings and predatory flies. Despite this IGP, the presence of *H. axyridis* and *C. septempunctata* had a positive impact on soybean aphid biological control.

### *Biocontrol services at the landscape scale*

My work illustrates that to understand biological control we must consider the influence of both landscape and within-field community dynamics. Landscapes contain source and sink populations of natural enemies. My data show that semi-natural habitats such as forests and grasslands are positively correlated with species abundance and biocontrol services in soybean, thus these habitats are likely to serve as source populations which supply organisms to agroecosystems. As landscape diversity has a significant positive correlation with biocontrol services, maintaining overall landscape diversity, and especially the presence of perennial grassland and forested habitats in the landscape, will favor suppression of soybean aphid.

However, to advance biological control of *A. glycines,* we must also begin examining the landscape distribution of the primary host plant of this pest, buckthorn species in the genus *Rhamnus*. *Rhamnus cartharica and R. frangula* are widely distributed exotic shrubs which invades forest edges, ditches and fencerows (Voegtlin et al. 2004, Voegtlin et al. 2005). These plants are more abundant in northern sections of the invasive range of *A. glycines*. Since its detection in 2000, soybean aphid has often been detected and reached threshold earlier in the season in areas with an abundance of buckthorn. Soybean fields in southern Ohio, Illinois, Indiana, and Iowa where buckthorn is less abundant or absent often see alate flights later in the season. It is thought that these aphids are migrating from northern fields into these areas. A critical next step in soybean aphid biological control research is to determine if the abundance and distribution of buckthorn in the landscape influences the establishment and population dynamics of soybean aphid in soybean and at what spatial scale.

Although my work has concentrated on the biological control of soybean aphid, the positive correlation between landscape diversity and biocontrol services is likely to apply to other pests in agricultural habitats. The generalist natural enemies found in soybean fields are also important antagonists of many other herbivores. To fully understand the influence of landscape on biocontrol services, it should be measured in multiple habitats. I have begun to develop a sentinel measure of biocontrol services using corn earworm eggs which can be deployed in multiple habitats to measure the activity of natural enemies. This will yield information on the landscape-wide biocontrol service provided by natural enemies.

This is a critical time to understand the influence of semi-natural habitats on natural enemy abundance and biocontrol services. Currently, corn acreage is on the rise in response to increased demand for corn ethanol, with harvested acres rising by 15 million acres between 2006 and 2007 (NASS 2008). Increasing pressure to produce biofuel crops on agricultural lands could have a negative effect on biocontrol services in these landscapes particularly if corn production increases, reducing landscape diversity and displacing habitats associated with greater predator abundance. Our focus must be on how these landscape changes will affect arthropod biodiversity, pollination and pest management in food and biofuel crops. There is likely to be major differences in the sustainability of annual monoculture biofuel crops such as corn grain compared with perennial polyculture crops such as prairie mimics.

### *Landscape scale approach to native species conservation*

In addition to measuring biocontrol services, my work also illustrated a potential negative outcome of soybean aphid biological control: the loss of native coccinellid species due to competition from exotic species. While I illustrated that the exotic species *H. axyridis* and *C. septempunctata* are key in suppressing *A. glycines*, my work also illustrates that these coccinellids are intraguild predators of native species. Management plans for native species conservation must consider the role of landscape elements in influencing native species abundance and native and exotic species interactions. Grasslands appear to positively influence the abundance of native species.

Understanding the mechanism behind this pattern is the critical next step in preserving native coccinellid biodiversity. It is possible that native coccinellids are adapted to open savanna and prairie landscapes that formerly dominated large areas of the north-central U.S. and may still favor landscapes with open grasslands. However, this does not explain the decline in native coccinellids in the last few decades, long after landscapes were transformed by human settlement. Alternatively, native species may be able to thrive in landscapes that are less favorable to invasion by exotic Coccinellidae many of which are known to be strong intraguild predators. Since exotics are favored by forested habitat, a lack of these landscape elements in portions of Minnesota and Iowa may restrict the abundance and dominance of coccinellid communities by exotics in these areas. I propose that landscape structure may be limiting the success of *H. axyridis* and other exotics in intensely agricultural landscapes and allowing persistence of native coccinellid communities in such regions. If so, understanding the role of perennial grasslands in supporting source populations of native coccinellids is a conservation priority. We must determine if the different types of perennial grassland, such as pasturelands, restored prairies and abandoned old fields vary in their ability to support native species.

Within these habitats, understanding the role of competitive displacement and intraguild predation by exotics will be crucial in the conservation of native species. I began this work by investigating the extent of IGP that occurs within soybean fields. This work illustrates that, at least in soybean fields, it is not the intensity of IGP that is contributing to the decline in native coccinellids but more likely the structure of the predator guild consuming this resource. In landscapes that favor exotic coccinellids, native coccinellid eggs in soybean are more likely to be consumed by exotic predator guilds. This is likely contributing to the decline in several native coccinellid species in forested states such as Michigan were populations of *B. ursina*, *C. munda, C. stigma, and H. convergens* have noticeably declined (Colunga-Garcia and Gage 1998). Alternatively, despite overall equal egg predation in intensely agricultural landscapes such as Iowa, the presence of fewer exotic competitors is likely to favor the persistence of native coccinellid populations.

Although it is impossible to remove established exotic coccinellids from the environment, we can protect native biodiversity by protecting and promoting landscape attributes which favor native coccinellid populations. The majority of research on exotic and native coccinellids has focused on their populations in agricultural fields (Snyder and Evans 2006), which likely function as sink populations supplied by surrounding natural habitats. Future work must focus on understanding interactions between source populations of native and exotic coccinellids, in grassland and forested habitats.

# APPENDICES

## Appendix A

Table A1.1. Record of deposition of voucher specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 2008-07

Title of thesis or dissertation (or other research projects):

LANDSCAPE SCALE AND WITHIN-FIELD INFLUENCES ON PREDATOR ABUNDANCE AND BIOCONTROL SERVICES IN SOYBEAN FIELDS.

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums

Investigator's Name(s) (typed)

Mary M. Gardiner

Date 8-22-08

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24: 141-42.

Deposit as follows:

Original: Include as Appendix 1 in ribbon copy of thesis or dissertation.

Copies: Include as Appendix 1 in copies of thesis or dissertation.
Museum(s) files.
Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

# Appendix A

## Voucher Specimen Data

Page 1 of 7 Pages

| Species or other taxon | Label data for specimens collected or used and deposited | Number of: | | | | | | | Museum where deposited |
|---|---|---|---|---|---|---|---|---|---|
| | | Eggs | Larvae | Nymphs | Pupae | Adults ♀ | Adults ♂ | Other* | |
| **Carabidae** | | | | | | | | | |
| *Acupalpus partiarius* | Hancock, WI 7/8/2006 | | | | | | | 1 | MSU |
| *Agonum cupreum* | Breckenridge, MI 5/31/2005 | | | | | | | 1 | MSU |
| *Agonum octopunctatum* | Schoolcraft, MI 7/31/2006 | | | | | | | 1 | MSU |
| *Agonum cupripenne* | Schoolcraft, MI 8/7/2006 | | | | | | | 2 | MSU |
| | Schoolcraft, MI 7/31/2006 | | | | | | | 1 | MSU |
| | Breckenridge, MI 8/10/2006 | | | | | | | 1 | MSU |
| *Agonum placidum* | Schoolcraft, MI 8/7/2006 | | | | | | | 1 | MSU |
| | Schoolcraft, MI 7/24/2006 | | | | | | | 1 | MSU |
| | Hancock, WI 8/3/2006 | | | | | | | 1 | MSU |
| | Hancock, WI 8/11/2006 | | | | | | | 1 | MSU |
| | Sutherland, IA 8/18/2006 | | | | | | | 1 | MSU |
| | Arlington, WI 7/29/2005 | | | | | | | 1 | MSU |
| | Arlington, WI 8/5/2005 | | | | | | | 2 | MSU |
| *Amara aenae* | Schoolcraft, MI 7/5/2006 | | | | | | | 1 | MSU |
| | Schoolcraft, MI 7/24/2006 | | | | | | | 1 | MSU |
| | Hickory Corners, MI 7/5/2006 | | | | | | | 1 | MSU |
| | Hickory Corners, MI 7/10/2006 | | | | | | | 1 | MSU |

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Mary M. Gardiner

Date 8/22/2008

*All specimens are adults, sex unknown

Voucher No. 2008-07

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator 8/21/2008 Date

# Appendix A

## Voucher Specimen Data

Page 2 of 7 Pages

| Species or other taxon | Label data for specimens collected or used and deposited | Number of: | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Eggs | Larvae | Nymphs | Pupae | Adults ♀ | Adults ♂ | Other* | Museum where deposited |
| **Carabidae** | | | | | | | | | |
| *Anisodactylus rusticus* | Hickory Corners, MI 6/12/2006 | | | | | | | 2 | MSU |
| | Hickory Corners, MI 6/19/2006 | | | | | | | 1 | MSU |
| | Hickory Corners, MI 6/26/2006 | | | | | | | 1 | MSU |
| *Anisodactylus sanctaecrucis* | Hancock, WI 6/6/2006 | | | | | | | 1 | MSU |
| | Breckenridge, MI 7/6/2006 | | | | | | | 1 | MSU |
| | Breckenridge, MI 7/13/2006 | | | | | | | 1 | MSU |
| | Hancock, WI 7/17/2006 | | | | | | | 1 | MSU |
| *Bembidion femoratum* | Hancock, WI 7/4/2005 | | | | | | | 2 | MSU |
| | Hancock, WI 6/22/2006 | | | | | | | 1 | MSU |
| | Hancock, WI 7/11/2005 | | | | | | | 1 | MSU |
| *Bembidion nitidum* | Breckenridge, MI 6/14/2006 | | | | | | | 1 | MSU |
| | Breckenridge, MI 7/6/2006 | | | | | | | 1 | MSU |
| | Hancock, WI 7/9/2005 | | | | | | | 1 | MSU |
| | Hancock, WI 7/25/2005 | | | | | | | 1 | MSU |
| *Bembidion quadrimaculatum* | Hancock, WI 7/4/2005 | | | | | | | 1 | MSU |
| | Hancock, WI 7/15/2006 | | | | | | | 1 | MSU |
| | Rosemount, MN 7/7/2005 | | | | | | | 1 | MSU |

(Use additional sheets if necessary)
Investigator's Name(s) (typed)

Mary M. Gardiner

Date 8/22/2008

*All specimens are adults, sex unknown

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# Appendix A

## Voucher Specimen Data

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| Species or other taxon | Label data for specimens collected or used and deposited | Number of: Eggs | Larvae | Nymphs | Pupae | Adults ♀ | Adults ♂ | Other* | Museum where deposited |
|---|---|---|---|---|---|---|---|---|---|
| **Carabidae** | | | | | | | | | |
| *Bembidion quadrimaculatum* | Rosemount, MN 7/21/2005 | | | | | | | 1 | |
| *Bembidion rabidum* | Schoolcraft, MI 6/6/2005 | | | | | | | 1 | |
| *Bembidion obtusum* | Saginaw, MI 7/19/2006 | | | | | | | 1 | |
| *Brachinus ovipennis* | Saginaw, MI 6/22/2006 | | | | | | | 1 | |
| *Calathus gregarius* | Lucus, IA 6/21/2006 | | | | | | | 1 | |
| | Hickory Corners, MI 6/19/2006 | | | | | | | 1 | |
| *Chlaenius sericeus* | Schoolcraft, MI 8/2/2005 | | | | | | | 1 | |
| *Chlaenius pusillus* | Ames, IA 6/6/2006 | | | | | | | 1 | |
| | Ames, IA 6/15/2006 | | | | | | | 1 | |
| | Nashua, IA 6/17/2006 | | | | | | | 1 | |
| | Nashua, IA 7/31/2006 | | | | | | | 1 | |
| *Chlaenius tricolor* | Nashua, IA 7/17/2006 | | | | | | | 1 | |
| | Nashua, IA 7/24/2006 | | | | | | | 1 | |
| | Hancock, WI 8/3/2006 | | | | | | | 1 | |
| | Schoolcraft, MI 8/1/2006 | | | | | | | 1 | |
| *Clivina bipustulata* | Saginaw, MI 6/15/2005 | | | | | | | 1 | |

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Mary M. Gardiner

Date 8/22/2008

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Curator Date

*All specimens are adults, sex unknown

# Appendix A

## Voucher Specimen Data

Page 4 of 7 Pages

| Species or other taxon | Label data for specimens collected or used and deposited | Number of: | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Eggs | Larvae | Nymphs | Pupae | Adults ♀ | Adults ♂ | Other* | Museum where deposited |
| **Carabidae** | | | | | | | | | |
| *Clivina bipustulata* | Saginaw, MI 6/22/2005 | | | | | | | 1 | MSU |
| *Clivina impressefrons* | Hickory Corners, MI 6/20/2005 | | | | | | | 1 | MSU |
| *Clivina* spp. | Hancock, WI 7/4/2005 | | | | | | | 1 | MSU |
| *Cyclotrachelus sodalis* | Saginaw, MI 6/22/2005 | | | | | | | 2 | MSU |
| *Dicaelus elongatus* | Nashua, IA 6/17/2006 | | | | | | | 1 | MSU |
| | Nashua, IA 7/17/2006 | | | | | | | 1 | MSU |
| *Dyschirius globulosus* | Rosemount, MN 6/16/2005 | | | | | | | 1 | MSU |
| *Elaphropus anceps* | Hancock, WI 7/11/2005 | | | | | | | 1 | MSU |
| | Hancock, WI 7/25/2005 | | | | | | | 1 | MSU |
| | Hancock, WI 7/15/2006 | | | | | | | 1 | MSU |
| | Hancock, WI 7/25/2006 | | | | | | | 1 | MSU |
| *Galerita janus* | Lucus, IA 7/19/2006 | | | | | | | 1 | MSU |
| *Geopinus incrassatus* | Hancock, WI 6/15/2006 | | | | | | | 4 | MSU |
| *Harpalus affinis* | Saginaw, MI 6/15/2005 | | | | | | | 1 | MSU |
| *Harpalus caliginosus* | Sutherland, IA 7/28/2006 | | | | | | | 1 | MSU |
| *Harpalus erraticus* | Hancock, WI 8/3/2006 | | | | | | | 2 | MSU |
| *Harpalus herbaivagus* | Hancock, WI 6/14/2006 | | | | | | | 1 | MSU |

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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# Appendix A

## Voucher Specimen Data

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| | | | Number of: | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species or other taxon | Label data for specimens collected or used and deposited | | Eggs | Larvae | Nymphs | Pupae | Adults ♀ | Adults ♂ | Other* | Museum where deposited |
| **Carabidae** | | | | | | | | | | |
| *Harpalus herbaivagus* | Hancock, WI | 7/8/2006 | | | | | | | 1 | MSU |
| *Harpalus persylvanicus* | Saginaw, MI | 6/15/2005 | | | | | | | 2 | MSU |
| *Lebia fuscata* | Schoolcraft, MI | 6/6/2005 | | | | | | | 1 | MSU |
| *Lebia spp.* | Lucas, IA | 6/6/2006 | | | | | | | 1 | MSU |
| | Ames, IA | 6/20/2006 | | | | | | | 1 | MSU |
| *Poecilus chalcites* | Breckenridge, MI | 6/15/2005 | | | | | | | 2 | MSU |
| *Poecilus lucublandus* | Lucas, IA | 6/6/2006 | | | | | | | 1 | MSU |
| *Pterostichus commutabilis* | Ames, IA | 6/6/2006 | | | | | | | 1 | MSU |
| *Pterostichus melanarius* | Breckenridge, MI | 6/15/2005 | | | | | | | 1 | MSU |
| | Breckenridge, MI | 6/22/2005 | | | | | | | 1 | MSU |
| *Pterostichus permundus* | Saginaw, MI | 6/22/2005 | | | | | | | 1 | MSU |
| | Breckenridge, MI | 6/22/2005 | | | | | | | 1 | MSU |
| *Scarites quadriceps* | Breckenridge, MI | 5/31/2005 | | | | | | | 1 | MSU |
| | Breckenridge, MI | 6/8/2005 | | | | | | | 1 | MSU |
| *Stenolophus comma* | Breckenridge, MI | 6/8/2005 | | | | | | | 1 | MSU |
| *Stenolophus ochropezus* | Lucas, IA | 7/5/2006 | | | | | | | 1 | MSU |
| *Synchus impunctatus* | Hancock, WI | 6/14/2006 | | | | | | | 1 | MSU |

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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Date 8/22/2008

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# Appendix A

## Voucher Specimen Data

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| Species or other taxon | Label data for specimens collected or used and deposited | Number of: Eggs | Larvae | Nymphs | Pupae | Adults ♀ | Adults ♂ | Other* | Museum where deposited |
|---|---|---|---|---|---|---|---|---|---|
| *Trechus quadristriatus* | Saginaw, MI 6/15/2005 | | | | | | | 1 | MSU |
| **Coccinellidae** | | | | | | | | | |
| *Harmonia axyridis* | Breckenridge, MI 7/15/2005 | | | | | | | 1 | MSU |
| *Coccinellia septempunctata* | Saginaw, MI 7/15/2005 | | | | | | | 1 | MSU |
| *Coleomegilla maculata* | Saginaw, MI 7/21/2005 | | | | | | | 1 | MSU |
| *Hippodamia parenthesis* | Breckenridge, MI 8/16/2005 | | | | | | | 1 | MSU |
| *Hippodamia variegata* | East Lansing, MI 8/24/2005 | | | | | | | 3 | MSU |
| *Collops nigriceps* | Prairie City, IA 7/10/2007 | | | | | | | 3 | MSU |
| **Syrphidae** | East Lansing, MI 8/24/2005 | | | | | | | 2 | MSU |
| **Chrysopidae** | East Lansing, MI 8/24/2004 | | | | | | | 1 | MSU |
| **Nabidae** | East Lansing, MI 8/24/2004 | | | | | | | 2 | MSU |
| **Lycosidae** | | | | | | | | | MSU |
| *Schizocosa crassipes* | Nashua, IA 6/17/2006 | | | | | | 1 | | MSU |
| *Schizocosa avida* | Breckenridge, MI 6/29/2005 | | | | | | 1 | | MSU |
| *Hogna helluo* | Ames, IA 6/30/2006 | | | | | | 1 | | MSU |
| *Trochosa terricola* | Sutherland, IA 7/13/2006 | | | | | | 1 | | MSU |
| *Pardosa saxatilis* | Saginaw, MI 7/26/2006 | | | | | | 1 | | MSU |
| **Linyphiidae** | Schoolcraft, MI 6/20/2005 | | | | | | 1 | | MSU |
| **Salticidae** | Saginaw, MI 6/8/2006 | | | | | | 1 | | MSU |

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

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# Appendix A

## Voucher Specimen Data

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| Species or other taxon | Label data for specimens collected or used and deposited | Number of: Eggs | Number of: Larvae | Number of: Nymphs | Number of: Pupae | Number of: Adults ♀ | Number of: Adults ♂ | Number of: Other* | Museum where deposited |
|---|---|---|---|---|---|---|---|---|---|
| **Thomisidae** | Ames, IA 6/22/2005 | | | | | | 1 | | MSU |

(Use additional sheets if necessary)
Investigator's Name(s) (typed)

Mary M. Gardiner

Date 8/22/2008

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# Appendix B

Table B1.1. Appendix B includes land cover maps for all field sites sampled in 2005 and 2006 in Iowa, Michigan, Minnesota and Wisconsin. Land cover is grouped into categories used in the principal component analyses presented in chapters 3-5. Below, the figure number, location, study year, and diversity of each site is listed.

| Study Site and Season | | | | Coordinates of Field Center | | |
|---|---|---|---|---|---|---|
| Figure # | State | Location | Year | N | W | Simpson's D |
| B1.1 | IA | Ames | 2005 | 41° 58' 50.60" | 93° 38' 13.86" | 4.35 |
| B1.2 | IA | Ames | 2006 | 41° 58' 48.91" | 93° 38' 49.42" | 4.19 |
| B1.3 | IA | Lucas | 2005 | 40° 58' 25.75" | 93° 24' 54.64" | 3.96 |
| B1.4 | IA | Lucas | 2006 | 40° 57' 43.47" | 93° 24' 04.54" | 4.82 |
| B1.5 | IA | Nashua | 2005 | 42° 55' 46.98" | 92° 33' 57.72" | 3.81 |
| B1.6 | IA | Nashua | 2006 | 42° 56' 07.99" | 92° 34' 22.75" | 3.44 |
| B1.7 | IA | Sutherland | 2005 | 42° 55' 37.99" | 95° 31' 53.18" | 2.68 |
| B1.8 | IA | Sutherland | 2006 | 42° 55' 50.06" | 95° 32' 17.52" | 2.43 |
| B1.9 | MI | Breckenridge | 2005 | 43° 22' 51.35" | 84° 31' 33.94" | 4.50 |
| B1.10 | MI | Breckenridge | 2006 | 43° 23' 01.09" | 84° 31' 33.58" | 5.11 |
| B1.11 | MI | Britton | 2006 | 41° 56' 18.62" | 83° 48' 27.53" | 3.28 |
| B1.12 | MI | East Lansing | 2006 | 42° 41' 26.34" | 84° 29' 37.68" | 4.07 |
| B1.13 | MI | Elsie | 2006 | 43° 4' 3.86" | 84° 29' 0.57" | 6.07 |
| B1.14 | MI | Hickory Corners | 2005 | 42° 24' 15.25" | 85° 22' 42.83" | 5.61 |
| B1.15 | MI | Hickory Corners | 2006 | 42° 24' 23.86" | 85° 23' 16.64" | 6.40 |
| B1.16 | MI | Monroe | 2006 | 41° 56' 56.22" | 83° 28' 13.43 | 5.15 |
| B1.17 | MI | Saginaw | 2005 | 43° 23' 10.89" | 84° 06' 49.96" | 5.28 |
| B1.18 | MI | Saginaw | 2006 | 43° 22' 41.39" | 84° 06' 49.94" | 5.36 |
| B1.19 | MI | Schoolcraft | 2005 | 42° 07' 45.66" | 85° 36' 42.02" | 5.70 |
| B1.20 | MI | Schoolcraft | 2006 | 42° 07' 41.04" | 85° 36' 50.01" | 5.55 |
| B1.21 | MI | Sheppard | 2006 | 43° 31' 33.11" | 84° 42' 18.88" | 5.51 |
| B1.22 | MI | Westphalia | 2006 | 42° 54' 51.58" | 84° 48' 50.60" | 4.95 |
| B1.23 | MN | Lamburton | 2005 | 44° 08' 29.31" | 95° 10' 30.10" | 2.73 |
| B1.24 | MN | Lamburton | 2006 | 44° 14' 32.72" | 95° 17' 32.02" | 3.51 |
| B1.25 | MN | Rosemount | 2005 | 44° 43' 57.94" | 93° 06' 20.25" | 4.60 |
| B1.26 | MN | Rosemount | 2006 | 44° 42' 13.32" | 93° 06' 23.76" | 4.53 |
| B1.27 | WI | Arlington | 2005 | 43° 18' 59.94" | 89° 20' 05.85" | 2.78 |
| B1.28 | WI | Arlington | 2006 | 43° 17' 44.72" | 89° 23' 00.94" | 3.35 |
| B1.29 | WI | Hancock | 2005 | 44° 06' 01.87" | 89° 32' 4.91" | 4.04 |
| B1.30 | WI | Hancock | 2006 | 44° 07' 06.72" | 89° 32' 35.72" | 5.56 |
| B1.31 | WI | Menominee | 2006 | 44° 58' 31.80" | 88° 27' 43.22" | 2.64 |
| B1.32 | WI | West Madison | 2005 | 43° 03' 51.77" | 89° 32' 18.52" | 2.55 |
| B1.33 | WI | West Madison | 2006 | 43° 04' 04.49" | 89° 32' 38.17" | 2.95 |

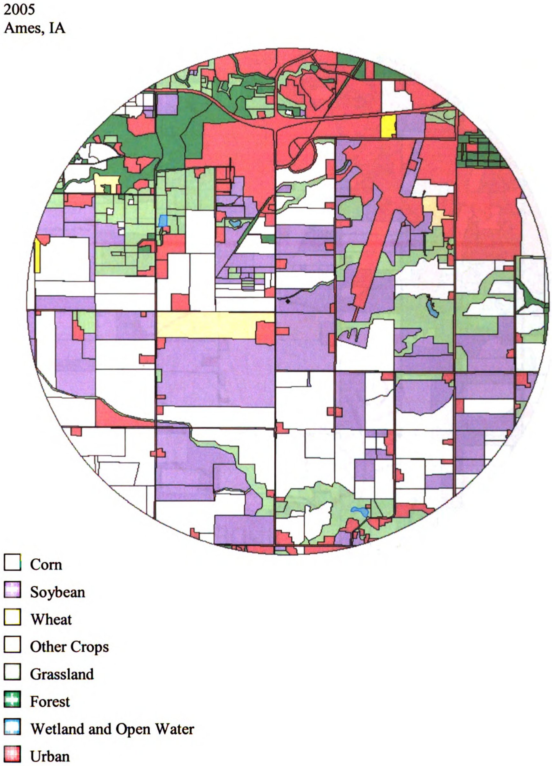


Figure B1.1. Land cover map of Ames IA, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Ames, IA

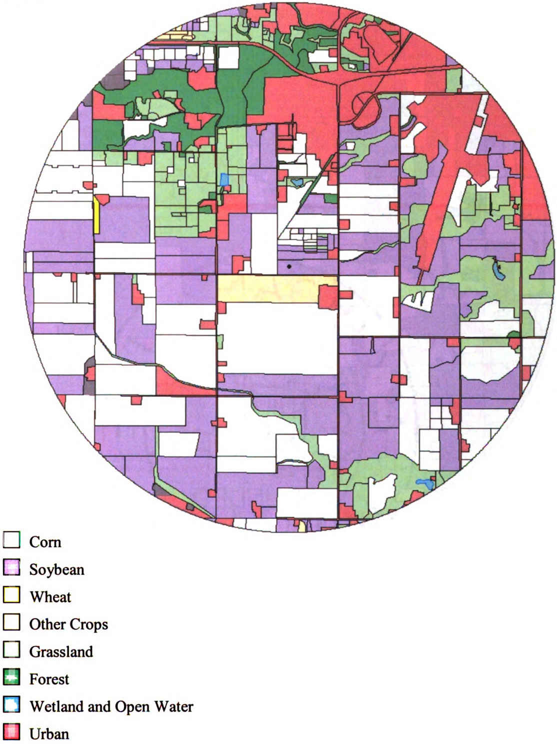
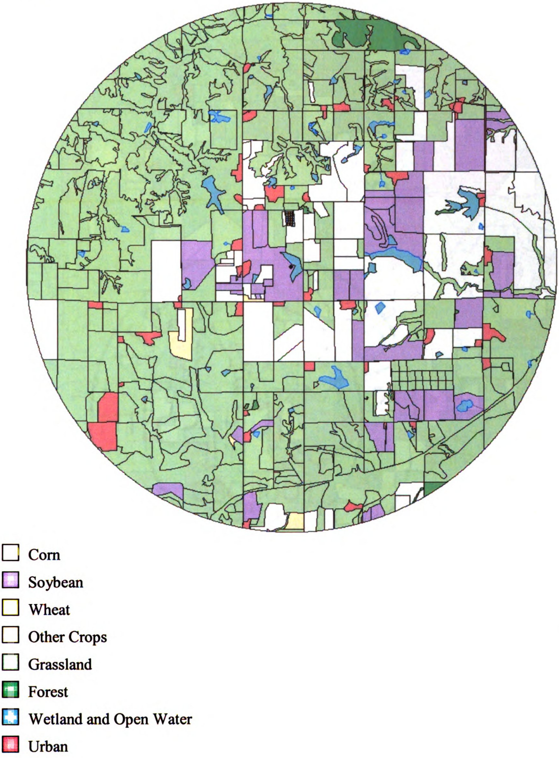


Figure B1.2. Land cover map of Ames IA, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.



2005
Lucas, IA

Figure B1.3. Land cover map of Lucas IA, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Lucas, Iowa

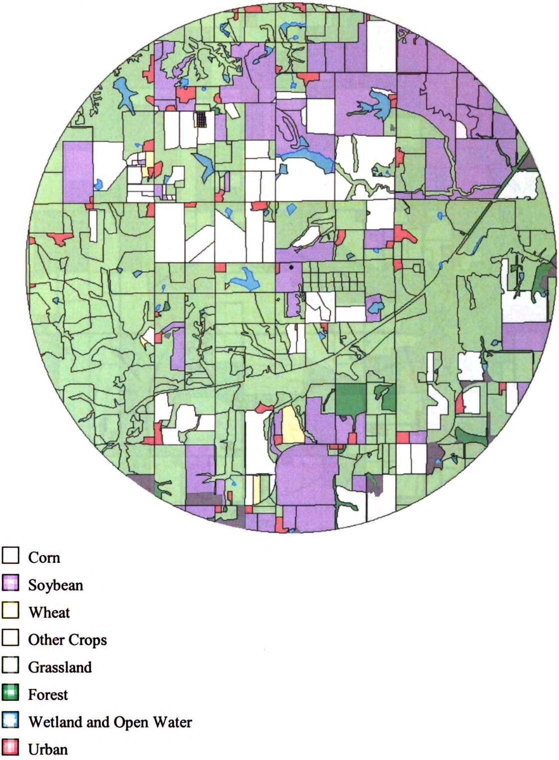


Figure B1.4. Land cover map of Lucas IA, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Nashua, Iowa

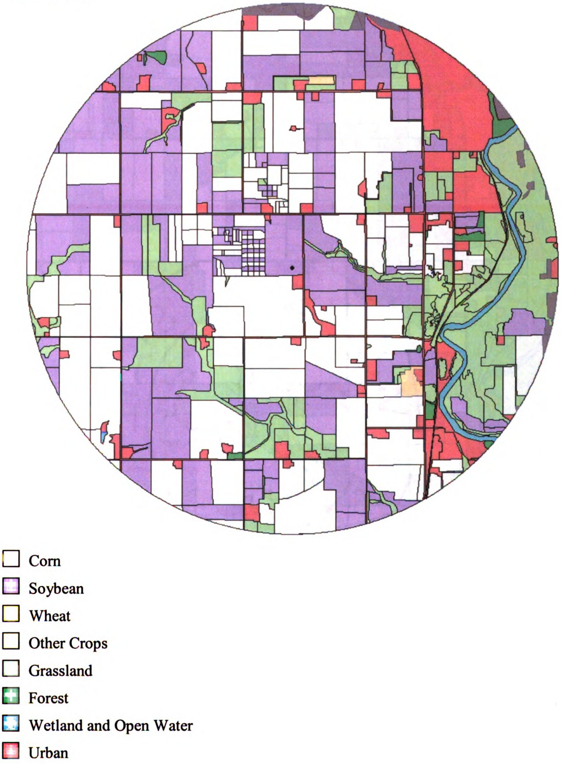
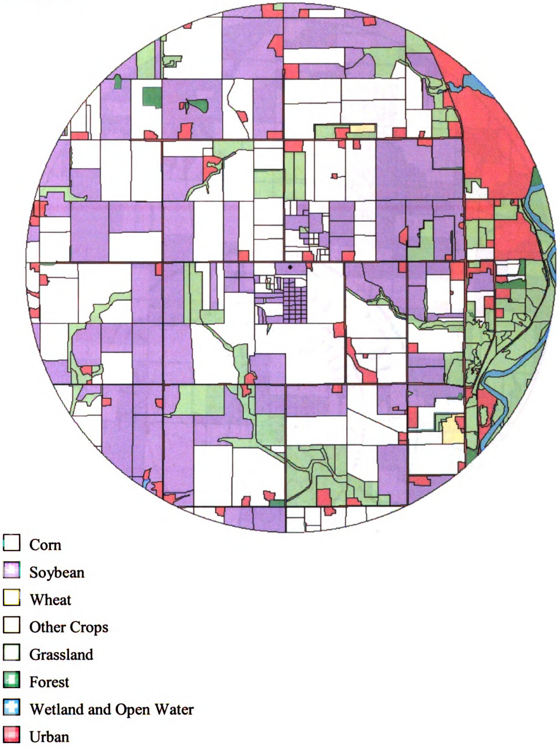


Figure B1.5. Land cover map of Nashua IA, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.



2006
Nashua, Iowa

Figure B1.6. Land cover map of Nashua IA, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Sutherland, Iowa

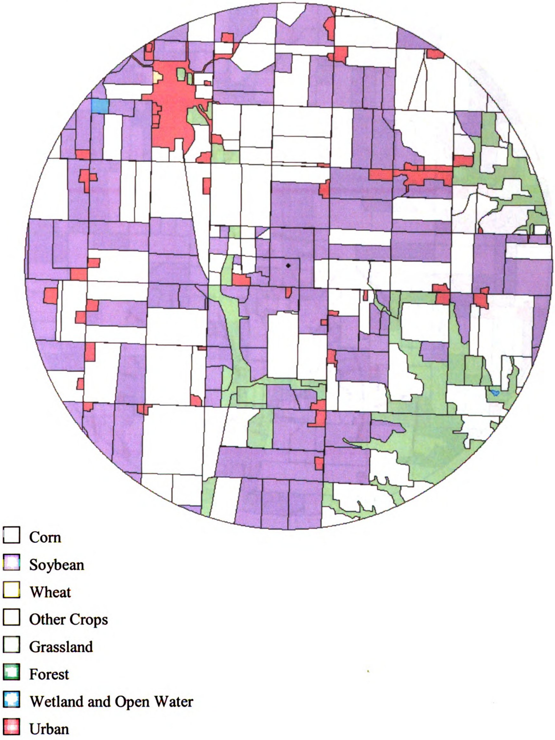


Figure B1.7. Land cover map of Sutherland IA, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Sutherland, Iowa

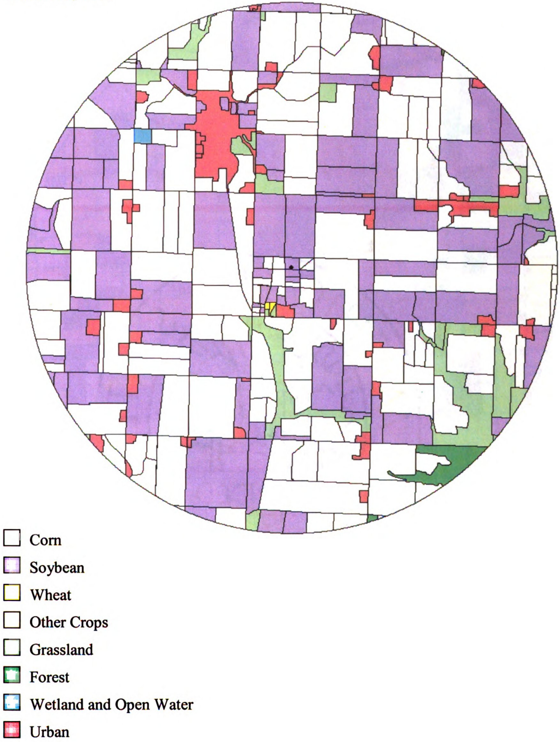
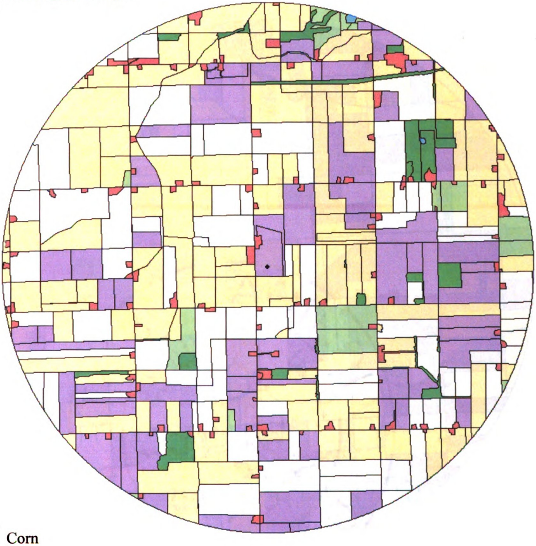


Figure B1.8. Land cover map of Sutherland, IA, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Breckenridge, Michigan

Figure B1.9. Land cover map of Breckenridge, MI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Breckenridge, Michigan



☐ Corn

🟪 Soybean

🟨 Wheat

☐ Other Crops

☐ Grassland

🟩 Forest

🟦 Wetland and Open Water

🟥 Urban

Figure B1.10. Land cover map of Breckenridge, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Britton, Michigan

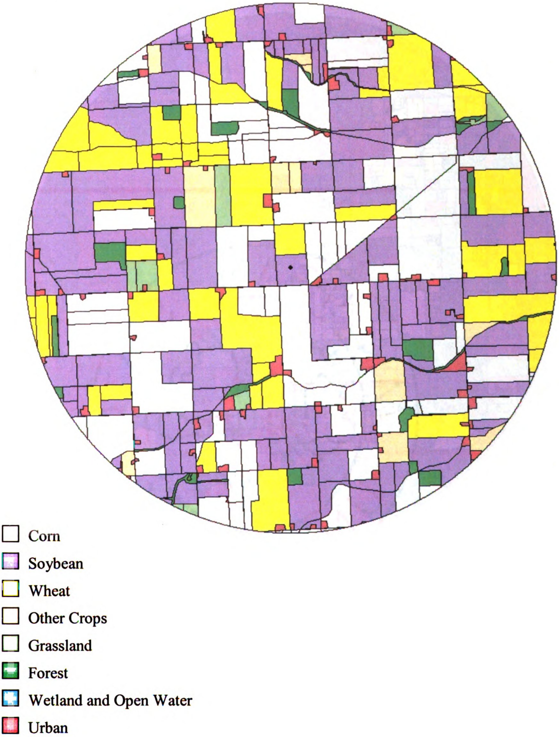


Figure B1.11. Land cover map of Britton, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
East Lansing, Michigan

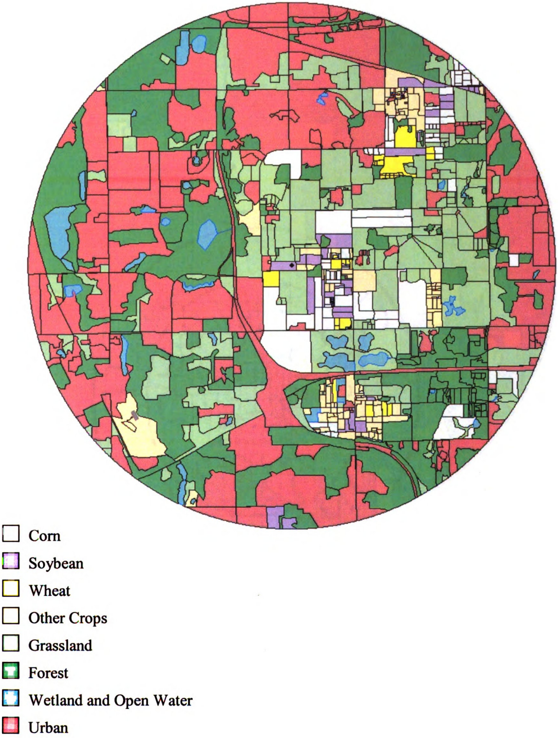


Figure B1.12. Land cover map of East Lansing, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Elsie, Michigan

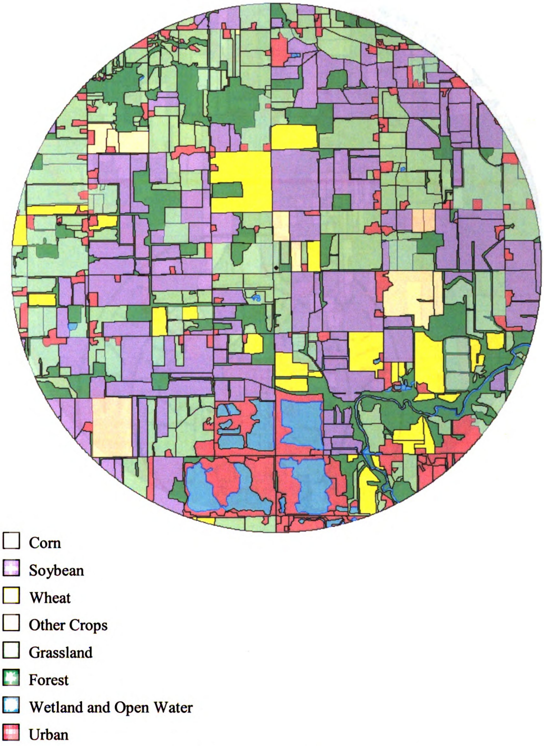


Figure B1.13. Land cover map of Elsie, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Hickory Corners, Michigan

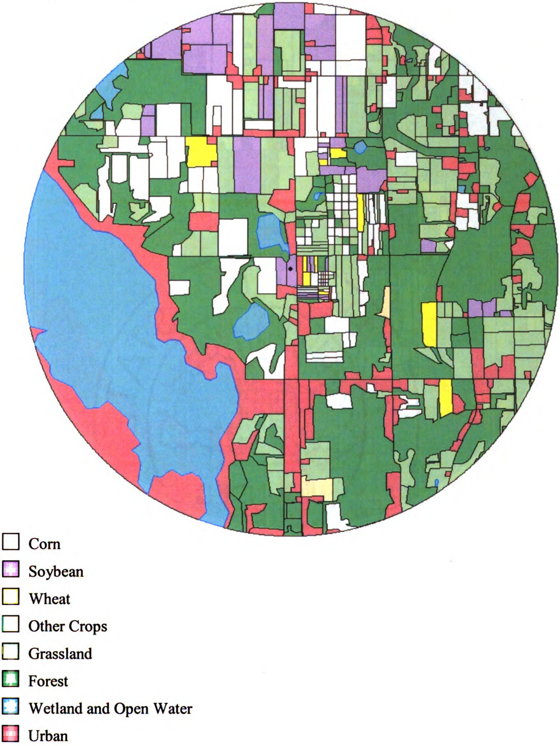
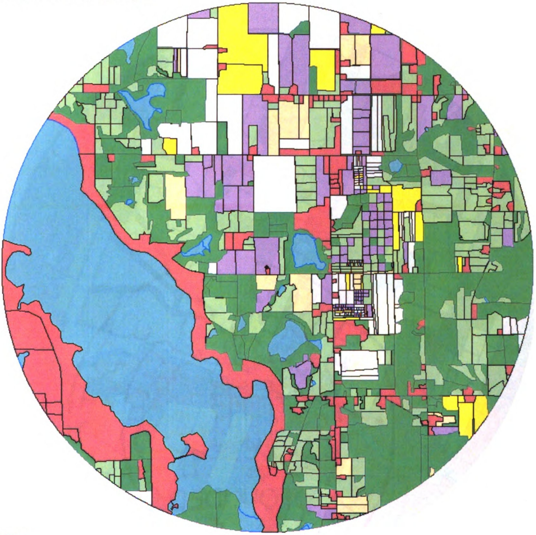


Figure B1.14. Land cover map of Hickory Corners, MI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

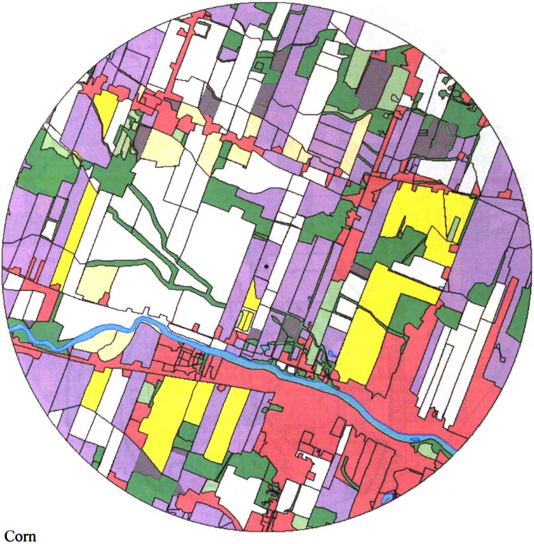
2006
Hickory Corners, Michigan



☐ Corn
🟪 Soybean
☐ Wheat
☐ Other Crops
☐ Grassland
🟩 Forest
🟦 Wetland and Open Water
🟥 Urban

Figure B1.15. Land cover map of Hickory Corners, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Monroe, Michigan



☐ Corn
🟪 Soybean
☐ Wheat
☐ Other Crops
☐ Grassland
🟩 Forest
🟦 Wetland and Open Water
🟥 Urban

Figure B1.16. Land cover map of Monroe, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Saginaw, MI

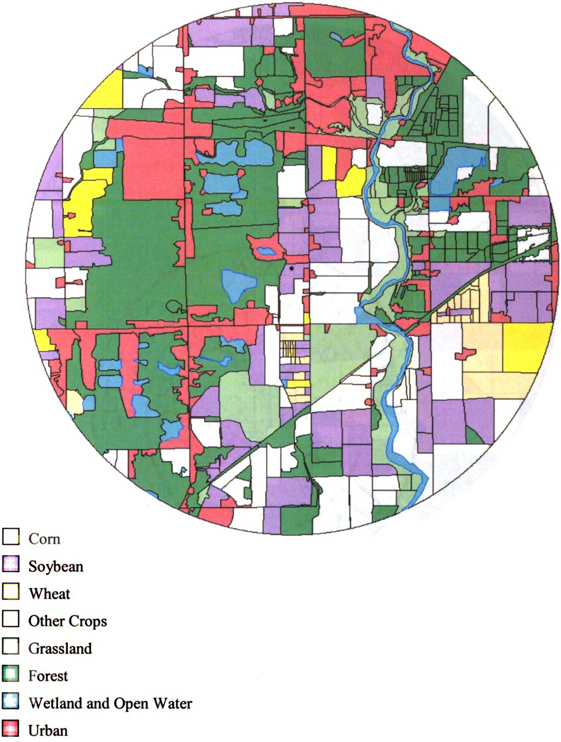


Figure B1.17. Land cover map of Saginaw, MI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Saginaw, Michigan

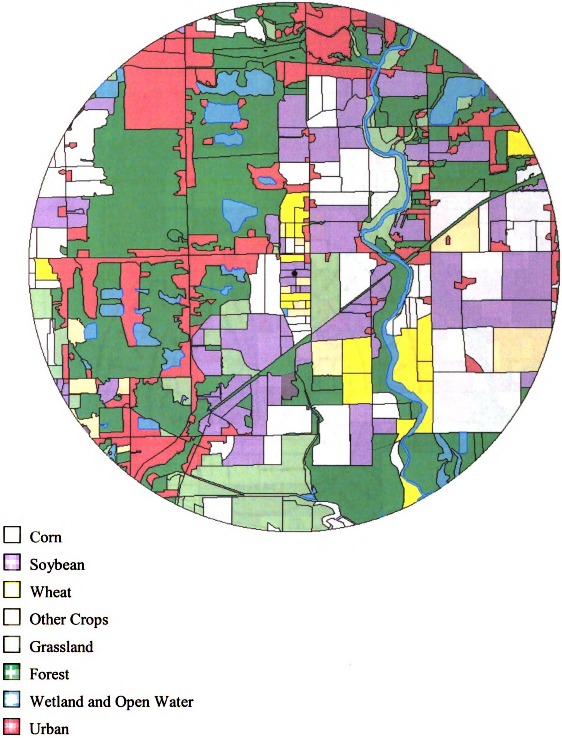


Figure B1.18. Land cover map of Saginaw, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Schoolcraft, MI

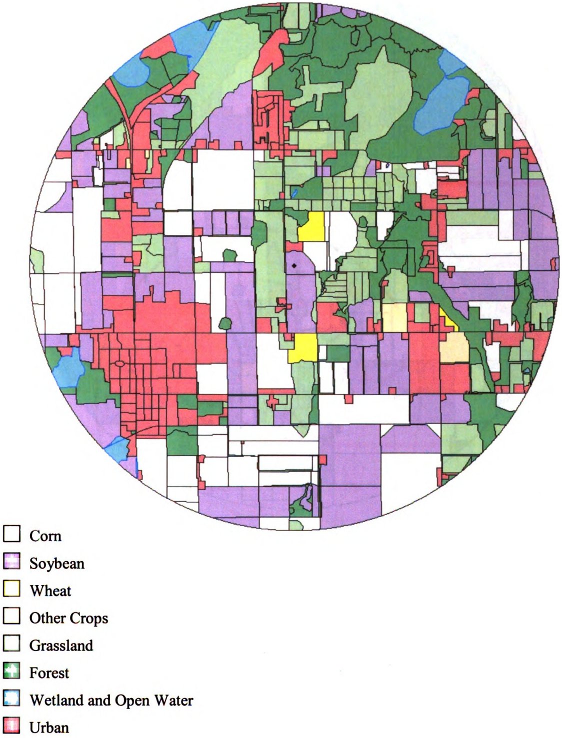
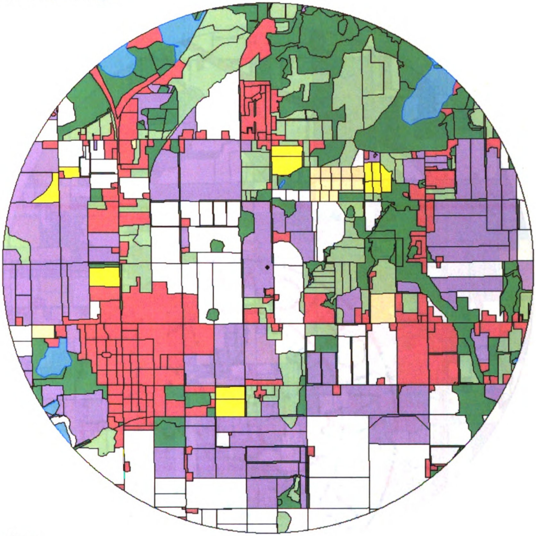


Figure B1.19. Land cover map of Schoolcraft, MI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Schoolcraft, Michigan



☐ Corn
🟪 Soybean
☐ Wheat
☐ Other Crops
☐ Grassland
🟩 Forest
🟦 Wetland and Open Water
🟥 Urban

Figure B1.20. Land cover map of Schoolcraft, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Shepherd, Michigan

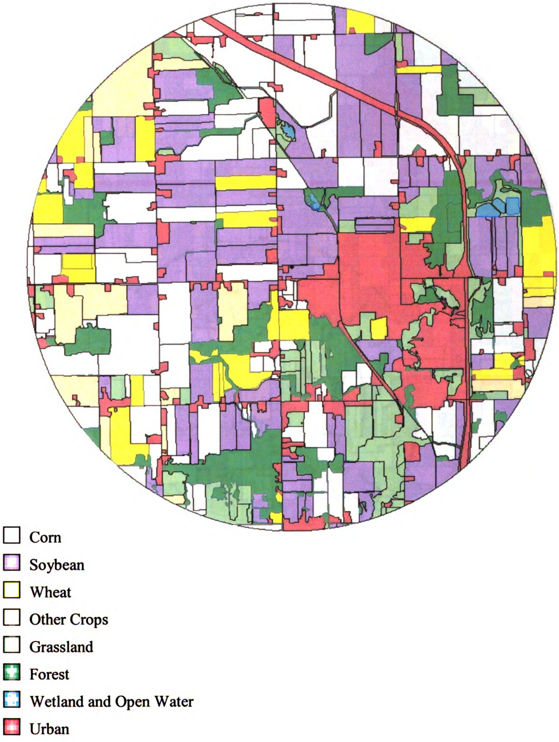


Figure B1.21. Land cover map of Shepherd, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Westphalia, Michigan

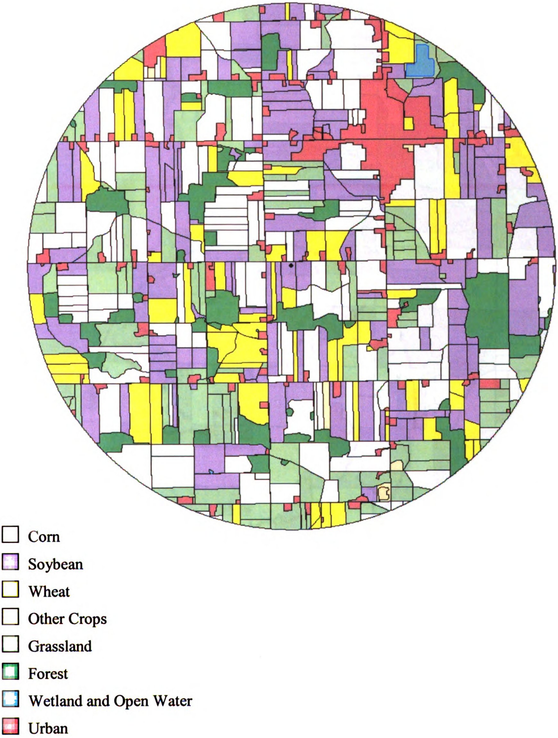


Figure B1.22. Land cover map of Westphalia, MI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Lamberton, Minnesota

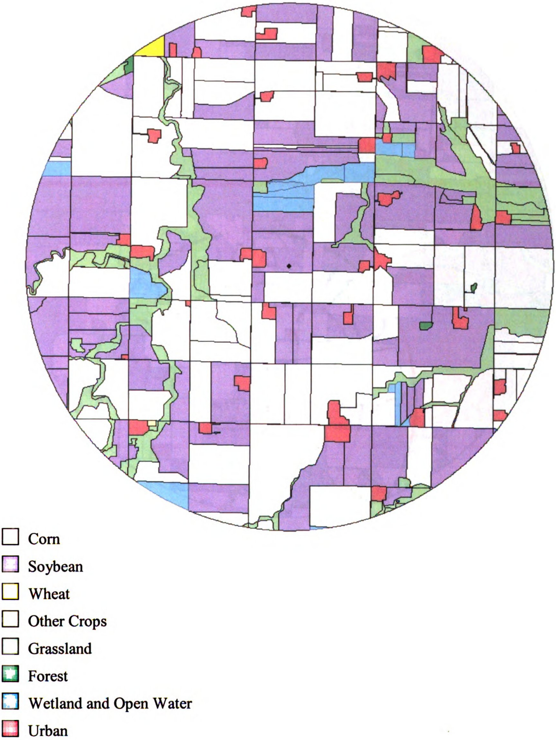
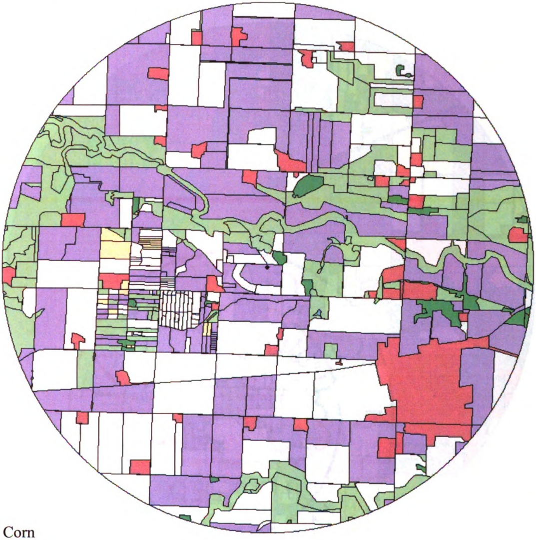


Figure B1.23. Land cover map of Lamberton, MN, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Lamberton, Minnesota



☐ Corn
🟪 Soybean
🟨 Wheat
☐ Other Crops
🟩 Grassland
🟩 Forest
🟦 Wetland and Open Water
🟥 Urban

Figure B1.24. Land cover map of Lamberton, MN, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Rosemount, Minnesota

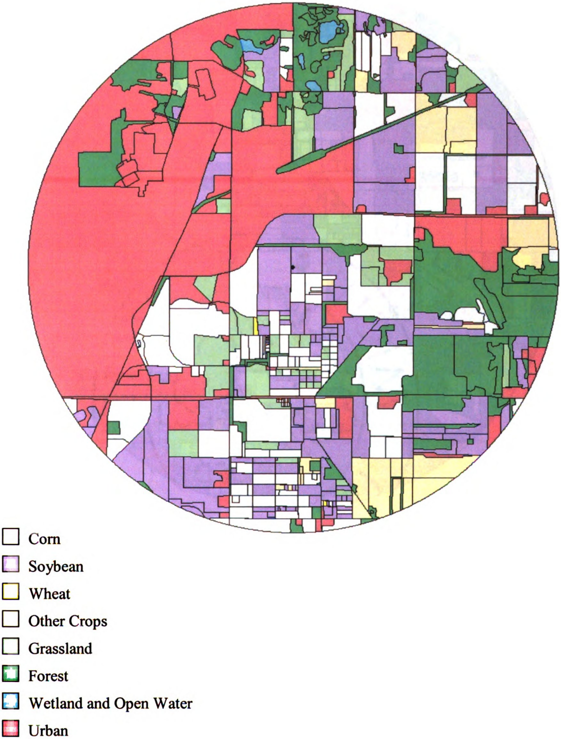


Figure B1.25. Land cover map of Rosemount, MN, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Rosemount, Minnesota

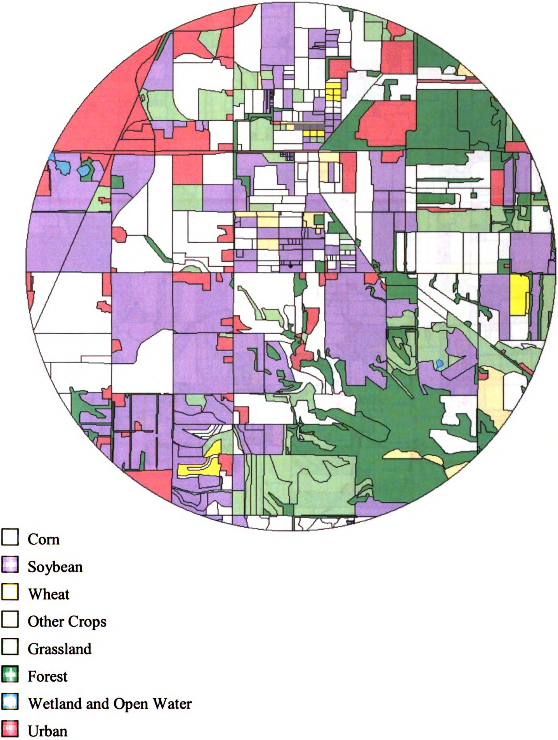


Figure B1.26. Land cover map of Rosemount, MN, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Arlington, Wisconsin

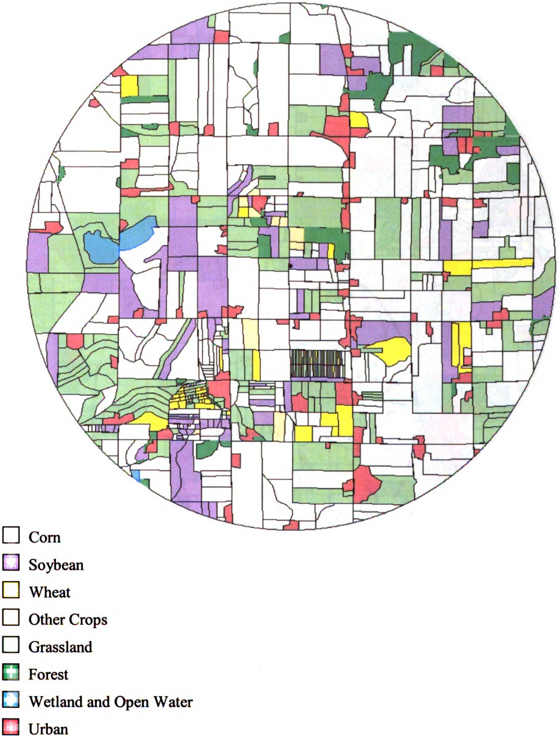
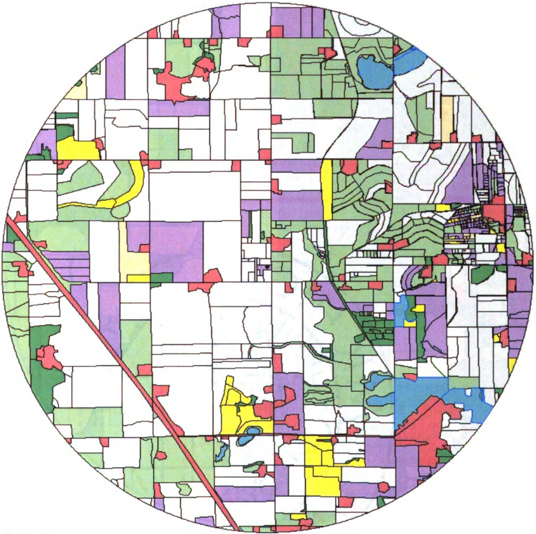


Figure B1.27. Land cover map of Arlington, WI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Arlington, Wisconsin



☐ Corn
🟪 Soybean
🟨 Wheat
☐ Other Crops
☐ Grassland
🟩 Forest
🟦 Wetland and Open Water
🟥 Urban

Figure B1.28. Land cover map of Arlington, WI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
Hancock, Wisconsin

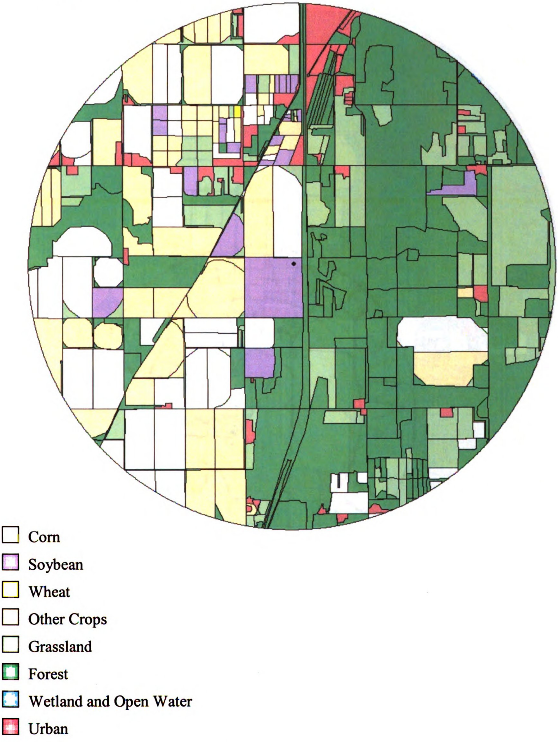


Figure B1.29. Land cover map of Hancock, WI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Hancock, Wisconsin

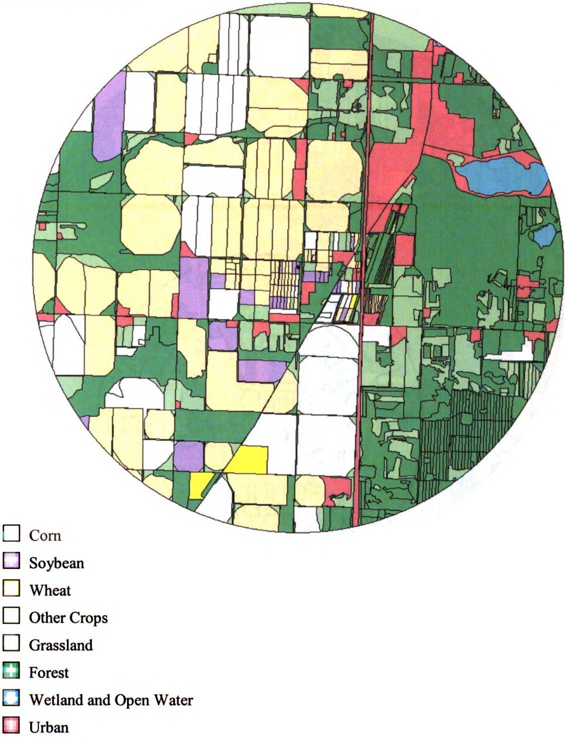
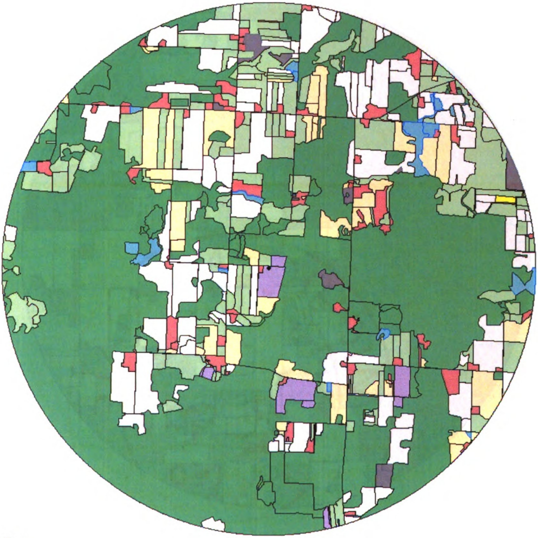


Figure B1.30. Land cover map of Hancock, WI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
Menominee, Wisconsin



☐ Corn
🟪 Soybean
☐ Wheat
☐ Other Crops
☐ Grassland
🟩 Forest
🟦 Wetland and Open Water
🟥 Urban

Figure B1.31. Land cover map of Menominee, WI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2005
West Madison, Wisconsin

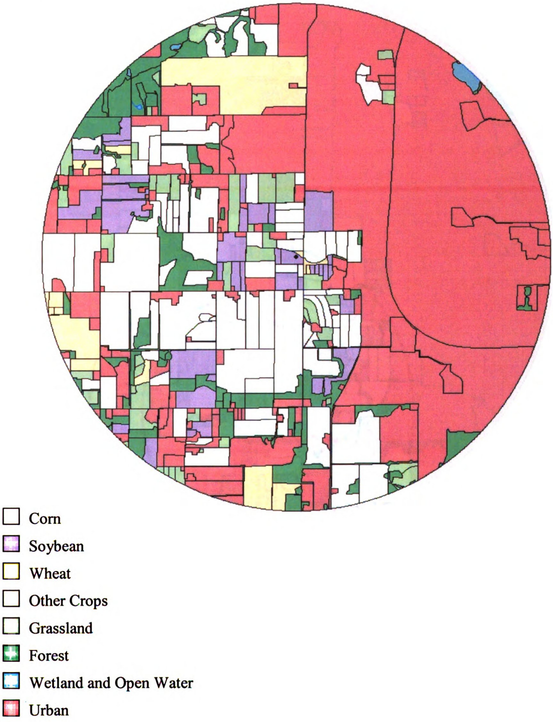


Figure B1.32. Land cover map of West Madison, WI, 2005. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

2006
West Madison, Wisconsin

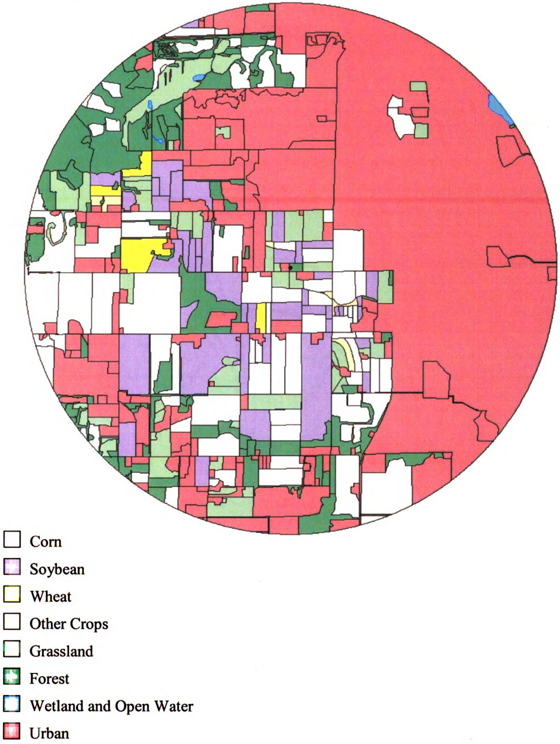


Figure B1.33. Land cover map of West Madison, WI, 2006. Focal soybean field indicated with dot in the center of the image. The landscape circle has a radius of 3.5 km.

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