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# Arthropod Diversity and Pest Suppression in Agricultural Landscapes

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Research at the Kellogg Biological Station Long-Term Ecological Research site (KBS LTER) is focused on understanding the ecological interactions underlying the productivity of row-crop ecosystems. Within these systems, insect pests and weeds represent two major groups of organisms that farmers must consistently and effectively manage. Since its inception in 1989, entomologists associated with KBS LTER have sought to develop a better understanding of the ecology of beneficial insects and the crop pests they control within agricultural landscapes. As a group, we have specifically focused on key taxa involved in pest suppression, namely, predators and parasitoids of insect herbivores and predators of weed seeds. The long-term goal of this work has been to inform agricultural practices that might enhance natural pest suppression and thus reduce the need for chemical pest controls. Working toward this goal has involved long-term observations coupled with shorter-term, hypothesis-driven experiments. This combination has proven a fruitful model for advancing science at KBS and the LTER Network in general (Knapp et al. 2012).

## Shifting Systems of Pest Management

For millennia, farmers have battled with weeds and insects to avoid crop losses. During the first half of the twentieth century, U.S. row-crop farmers primarily relied on natural enemies (predators and parasitoids of herbivores), cultural practices (e.g., tillage, rotation, variety selection), and a limited number of inorganic insecticides to help control insect pests. As a result, literature from that time is full of careful observations on the biology and ecology of both crop pests and their natural enemies. However, following the discovery of organochlorine insecticides during

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World War II, research on insect management rapidly shifted to a narrow focus on chemical control. These long-lasting and highly effective insecticides seemed a panacea, providing nearly complete control of even the most troublesome pests. Unfortunately, near sole reliance on chemical controls resulted in the development of insecticide resistance and decimation of natural enemy communities, and pest outbreaks followed, as did growing concerns over environmental impacts.

As early as 1959, Vernon Stern and colleagues began to call for the integration of chemical insecticides into a more holistic set of practices they termed "integrated control" (Stern et al. 1959). Their concept, now known as Integrated Pest Management (IPM), sought to combine cultural, biological, and chemical pest control in a systems approach. In response, researchers developed IPM systems that combined cultural tools like rotation and resistant varieties with biological controls including importation, conservation, and augmentation of natural enemies. Additionally, crops were regularly scouted and chemicals applied only after a pest population exceeded an economic threshold, that is, the population level at which action is needed to prevent an economic loss (Radcliffe et al. 2009).

More recently, the advent of genetically modified (GM) crops has once again shifted the focus in pest management. The development of field crops with built-in resistance to broad-spectrum herbicides—for example, glyphosate-tolerant soybean and corn—allowed a very different approach to weed management. Rather than scouting fields for weed species composition and growth stage and using selective herbicides, growers can now spray a single broad-spectrum herbicide whenever weeds reach critical levels. Moreover, farmers can also purchase "stacked" GM crop seeds that not only contain genes for herbicide resistance but also genes for producing bacterial toxins that confer resistance to multiple insect pests. Although it has simplified pest management for farmers, reliance on such a small set of tools has again yielded instances of resistance and concerns about environmental degradation (Ferry and Gatehouse 2009).

## Ecologically Based Pest Management

At the same time that agricultural scientists were developing new methods of pest management, ecologists were beginning to study agriculture from an ecological perspective (Lowrance et al. 1984, Carroll et al. 1990, Gliessman 1998, Robertson et al. 2004). One aspect of agroecology has focused on the question of how the biodiversity of cropping systems might be managed to achieve improved pest management (Altieri 1994). The relationship between biotic diversity and ecological performance has been a key question for ecologists for more than a half-century. Rooted in the diversity–stability arguments of the late twentieth century (MacArthur 1955, Elton 1958, Odum 1959, May 1973) and more recently in the study of biodiversity and ecosystem function (Schulze and Mooney 1993, Loreau et al. 2002), our understanding of the ways in which biodiversity influences ecosystem services continues to evolve. The study of predator–prey interactions has produced a rich body of theoretical and empirical work elucidating the influence of biotic diversity on herbivore population regulation (Ives et al. 2005, Bruno and Cardinale 2008, Letourneau et al. 2009).

Within this broader context, KBS LTER scientists have sought a deeper understanding of the interactions of beneficial insects and crop pests in agricultural landscapes.

## Determining Which Insects and Processes to Quantify

The KBS LTER Main Cropping System Experiment (MCSE) design was established in 1989 (Robertson and Hamilton 2015, Chapter 1 in this volume) and includes annual systems made up of corn (*Zea mays* L.)—soybean (*Glycine max* L.)—winter wheat (*Triticum aestivum* [L.]) rotations, alfalfa (*Medicago sativa* L.), hybrid poplars (*Populus* sp.), and unmanaged successional ecosystems (Table 8.1). Due to the long-term nature of the research, large 1-ha plots were established with five permanently located monitoring sites within each. From an entomological perspective, this sampling design presented both advantages and constraints. Fixed sampling points provide the opportunity to follow spatial patterns over time, but limit other types of investigations such as those involving dispersal and predator–prey interactions. From the outset, a nontrivial question has been which insects and ecological processes could best be studied within this framework.

A direct focus on insect herbivores was initially considered but ultimately set aside, primarily because each crop can support multiple species of insect pests and differences in pest life cycles and behaviors would require different, labor-intensive sampling strategies. In addition, many insect sampling approaches require destructive methods that would be at odds with other study objectives and themselves represent a disturbance to the ecosystems. Instead, we focused on insect predators and parasitoids that engage in biological regulation of insect herbivores, and in particular on predatory ladybird beetles (Coleoptera: Coccinellidae). Since 1989 coccinellids have been monitored in all MCSE systems at the main site and in selected portions of the surrounding landscape.

Logistical requirements suggested adoption of a simple sampling method that would minimally disturb the plant community but would capture the dynamics of coccinellid predators and foster understanding of their ecological function, both in time and space. A previous investigation of apple maggot (*Rhagoletis pomonella* Walsh) dispersal at KBS had successfully used transects of yellow sticky traps to determine flight paths of adult flies dispersing to an isolated orchard adjacent to the LTER main site (Ryan 1990). These sticky traps also captured many species of dispersing Coccinellidae. Maredia et al. (1992a) determined the optimal trap color to attract coccinellids and other key predators to be yellow, which was most attractive to *Coccinella septempunctata* (L.), the most abundant coccinellid, and equally as attractive as other colors to *Hippodamia parenthesis* (Say) and *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). As a result, yellow sticky traps (PHEROCON AM, Great Lakes IPM, Vestaburg, Michigan) have been deployed since 1988. A pole supports the traps 1 m above the soil surface (Maredia et al. 1992b) at each permanent sampling location. Traps are deployed for a minimum of 8 weeks each year from May to September in each replicate plot of the MCSE systems, for a total of 255 sample sites. Each is visited weekly to record the abundance of 17 species of Coccinellidae.

Table 8.1. Description of the KBS LTER Main Cropping System Experiment (MCSE).[a]

| Cropping System/Community | Dominant Growth Form | Management |
|---|---|---|
| *Annual Cropping Systems* | | |
| Conventional (T1) | Herbaceous annual | Prevailing norm for tilled corn–soybean–winter wheat (c–s–w) rotation; standard chemical inputs, chisel-plowed, no cover crops, no manure or compost |
| No-till (T2) | Herbaceous annual | Prevailing norm for no-till c–s–w rotation; standard chemical inputs, permanent no-till, no cover crops, no manure or compost |
| Reduced Input (T3) | Herbaceous annual | Biologically based c–s–w rotation managed to reduce synthetic chemical inputs; chisel-plowed, winter cover crop of red clover or annual rye, no manure or compost |
| Biologically Based (T4) | Herbaceous annual | Biologically based c–s–w rotation managed without synthetic chemical inputs; chisel-plowed, mechanical weed control, winter cover crop of red clover or annual rye, no manure or compost; certified organic |
| *Perennial Cropping Systems* | | |
| Alfalfa (T6) | Herbaceous perennial | 5- to 6-year rotation with winter wheat as a 1-year break crop |
| Poplar (T5) | Woody perennial | Hybrid poplar trees on a ca. 10-year harvest cycle, either replanted or coppiced after harvest |
| Coniferous Forest (CF) | Woody perennial | Planted conifers periodically thinned |
| *Successional and Reference Communities* | | |
| Early Successional (T7) | Herbaceous perennial | Historically tilled cropland abandoned in 1988; unmanaged but for annual spring burn to control woody species |
| Mown Grassland (never tilled) (T8) | Herbaceous perennial | Cleared woodlot (late 1950s) never tilled, unmanaged but for annual fall mowing to control woody species |
| Mid-successional (SF) | Herbaceous annual + woody perennial | Historically tilled cropland abandoned ca. 1955; unmanaged, with regrowth in transition to forest |
| Deciduous Forest (DF) | Woody perennial | Late successional native forest never cleared (two sites) or logged once ca. 1900 (one site); unmanaged |

[a]Site codes that have been used throughout the project's history are given in parentheses. Systems T1–T7 are replicated within the LTER main site; others are replicated in the surrounding landscape. For further details, see Robertson and Hamilton (2015, Chapter 1 in this volume).

Additional sampling regimes were overlaid on this basic design when other interesting pest–natural enemy associations were observed or uncovered by patterns in the predator trapping data. Over the years, pitfall traps have also been used to determine carabid (Coleoptera: Carabidae) beetle community structure (Clark et al. 1997), and the results coupled with long-term studies of the weed

seedbank (Gross et al. 2015, Chapter 7 in this volume) to better understand the role of insects in shaping weed community dynamics. Also, new invasive insects have been studied as they entered KBS, including herbivores such as the gypsy moth (*Lymnatria dispar* L.; Parry 2000, Kosola et al. 2001, Agrawal et al. 2002, Kosola et al. 2006), the soybean aphid (*Aphis glycines* Matsumura; Noma and Brewer 2007, 2008), and the exotic predaceous coccinellids *C. septempunctata* (Maredia et al. 1992b) and *Harmonia axyridis* Pallas, the multicolored Asian ladybird beetle (Colunga-Garcia and Gage 1998). In the remainder of this chapter, we present three case studies focusing on carabids, coccinellids, and the soybean aphid. Together, these examples encompass the breadth of insect studies conducted on site and illustrate some of the key lessons to be drawn from this long-term effort.

## Carabids in the KBS Landscape

Ground-dwelling beetles in the family Carabidae are a diverse and frequently studied taxon. With over 2500 species in North America, they inhabit nearly all terrestrial ecosystems and perform a variety of ecological functions as herbivores, carnivores, and omnivores. In agricultural ecosystems, carabids are best known as predators of insects, gastropods, and other invertebrates. However, many carabid species are omnivorous and some species feed mainly on seeds (granivores). In row-crop systems, carabids can thus provide significant pest suppression by consuming insect pests and weed seeds in the soil seed bank.

### *Carabid Response to Habitat*

Clark et al. (1997) first characterized the carabid communities of KBS LTER in the 5th and 6th years following MCSE establishment in 1989. They recorded 18 species, but 4 predatory species dominated and comprised 87% of the total catch. Pronounced differences in carabid communities occurred between the annual and perennial plant systems and between the Conventional and No-till systems. Management practices influenced habitat characteristics and served to structure the carabid communities in particular ways. For example, annual crop habitats contained significantly more *Poecilus lucoblandus* (Say) and *Agonum placidum* (Say), while the No-till and perennial crop systems favored *Cyclotrachelus sodalis* (Leconte).

Overall, Clark et al. (1997) concluded that no single system or habitat could be characterized as favoring carabid communities as a whole; rather, some systems and practices (e.g., tillage) favor particular species and disfavor others. Because carabids were frequently associated with feeding on crop insect pests, Clark et al. suggested there is potential for managing for selected carabid communities to enhance pest suppression.

### *Carabids and Weed Seed Predation*

Weed seedbanks can build over time and present a significant challenge for agronomic management of annual row crops. Menalled et al. (2001) observed that the

total abundance and number of weed species in the soil seedbank were increasing over a 6-year period (1993–1998) in the Conventional and No-till systems but declining in the Reduced Input and Biologically Based systems. Seedbank increases in the Conventional and No-till systems were dominated by annual grasses, and a later study by Menalled et al. (2007) found that carabid abundance and community structures responded to these changes. They found more total carabids in the Conventional than in the No-till and Biologically Based systems. However, granivores made up 32% of the total individuals captured in the No-till system but only 4 and 10% of total carabids in the Biologically Based and Conventional systems, respectively—implying that more resources were present for weed seed predators in the No-till system.

Menalled et al. (2007) tested this hypothesis by conducting seed removal experiments in these systems and found that predation on seeds of fall panicum (*Panicum dichotomiflorum* Michx.) and common lambsquarters (*Chenopodium album* L.) was (1) often more than twice as high in No-till compared to the Conventional and Biologically Based systems, particularly for fall panicum (Fig. 8.1), and (2) was closely correlated with seed predator captures ($r > 0.94$). Overall, these studies

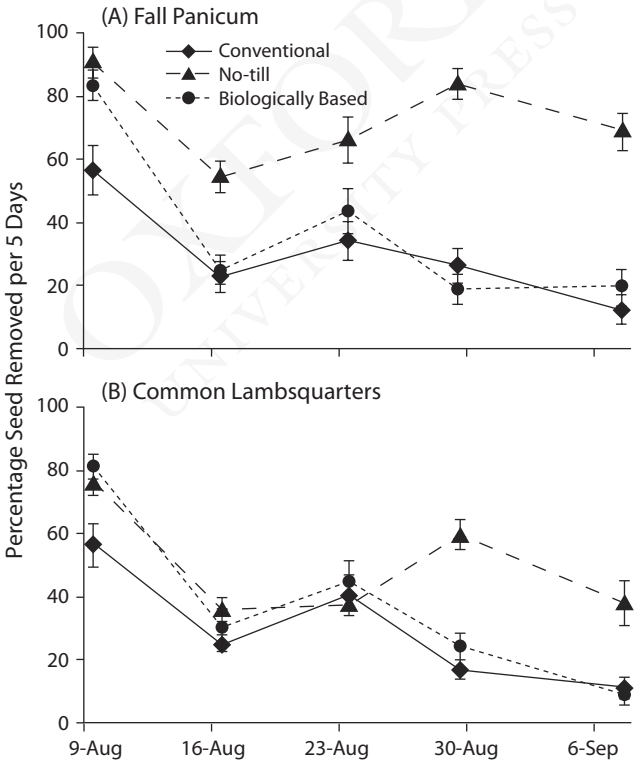


Figure 8.1. Percentage of seeds of (A) fall panicum and (B) common lambsquarters removed by invertebrate seed predators in three KBS LTER Main Cropping System Experiment (MCSE) systems during late summer of 2000 (mean ± SE, n = 6). Each data point represents a five-day period. Redrawn from Menalled et al. (2007) with permission from Elsevier.

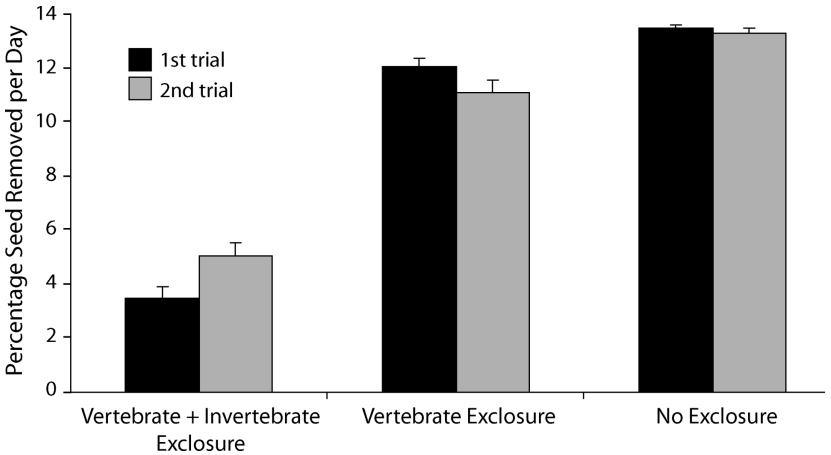


Figure 8.2. Percentage of weed seed removed per day in invertebrate + vertebrate exclosures, vertebrate exclosures, and without exclosure of seed predators (i.e., the control) in two trials averaged across field, species, and landscape type (mean ± SE). Redrawn from Menalled et al. (2000) with permission from Elsevier.

show that crop management affects carabid communities, which can in turn affect the weed seed bank through weed seed predation. Menalled et al. (2000) also studied weed seed predation by vertebrates vs. invertebrates in agricultural landscapes with increasing structural complexity. They found seed removal rates of between 7–12% per day, with invertebrates responsible for 50–66% of total predation (Fig. 8.2). They also identified a trend toward higher removal rates in more complex landscapes.

Overall, these studies suggest that carabid communities readily respond to changes in crop type and management (perennial vs. annual crops and tilled vs. no-till management). In turn, changes in community structure influence the ecosystem services that carabids provide—pest suppression and weed seed predation. However, probably due to the limited ability of carabids to disperse, changes in community structure at local scales do not always translate to similar effects at the landscape scale, as inconsistent impacts of landscape structure on weed seed predation have been observed. In the case of seed predation, this suggests that management efforts at the field and field-margin scale may more reliably influence carabid communities and services.

## Coccinellids in the KBS Landscape

Ladybird beetles, in the family Coccinellidae, are a major group of arthropod predators in agricultural landscapes (Obrycki et al. 2009). In addition to feeding on insect prey, many also consume nonprey foods including plant pollen and nectar (Lundgren 2009). Most overwinter as adults in noncrop habitats and disperse into crops in the spring in search of resources. After consuming sufficient prey, females

lay eggs; one or more generations occur per year based on the biology of individual species.

More than 20 years of sampling the coccinellid community of KBS has revealed a number of novel insights on the spatial and temporal patterns of insect predator responses to crop type and management practices. Our array of permanent geo-located sites has allowed scaling of analyses from microhabitat to landscape, and from individual weeks to seasonal to interannual change over two decades. Moreover, the spatial-temporal design of our insect observation program has provided the ability to quantify several unanticipated events, including the arrival of new herbivores and predators that, through long-range and local dispersal, entered the KBS landscape.

### *Characterizing the Coccinellid Community*

Maredia et al. (1992b) used a combination of sweep net, sticky trap, and visual observations to characterize the occurrence and relative abundance of predatory Coccinellidae at KBS LTER in 1989 and 1990. During that time period, they recorded 12 native and 1 exotic species (Table 8.2). Subsequent sticky trap sampling at the site has revealed the occurrence of one additional native species (*Hippodamia glacialis* [Fab.]) and documented the arrival of three additional exotic species (*Harmonia axyridis, Hippodamia variegata* [Goeze], and *Propylaea quatuordecimpunctata* [L.]), bringing the total to 13 native and 4 exotic species by 2009. Several native species have apparently declined in abundance since 1989–1990. For example, *Adalia bipunctata* (L.), *Chilocorus stigma* (Say), *H. convergens* Guérin-Meneville, and *Hippodamia parenthesis* (Say), all reported as common in 1989–1990, became rare by 2009. In addition, several species that were listed as occasionally observed in 1989–1990 fell below detectable levels by 2009, including *Anatis labiculata* (Say), *Coccinella novemnotata* Herbst, *Hippodamia tredecimpunctata tibialis* (Say), and *Hyperaspis undulata* (Say). Because Maredia et al. (1992b) used multiple collection methods and subsequent sampling only used sticky traps, it is uncertain if these represent true declines or sampling biases.

The exotic species *C. septempunctata*, which was intentionally released in Michigan in 1985 for control of aphids (Maredia et al. 1992b) and rapidly became a dominant species (Sirota 1990), was of particular interest to early LTER researchers. Maredia et al. (1992c) confirmed Sirota's (1990) observations that *C. septempunctata* was a univoltine (one generation per year) species in Michigan with peak adult populations occurring in mid- to late June. Wheat and alfalfa were found to be important early season habitats for *C. septempunctata*, likely because they contained aphid prey prior to spring-planted annual crops like corn and soybean. Later in the season, *C. septempunctata* dispersed throughout the landscape and was found in all MCSE systems but particularly in the Early Successional and Poplar systems that tended to have late season aphid infestations (Maredia et al. 1992b).

The LTER database also allows for coccinellid habitat preferences to be studied over longer periods of time, and examination of habitat use by nine species in MCSE systems from 1989 to 2007 reveals distinct patterns (Fig. 8.3). With the exception of *H. axyridis*, most species are found in greater abundance in one or

Table 8.2. Coccinellid species observed in the KBS landscape from 1989 to 2009.

| Species | Common Name, Lady Beetle | First Reported at LTER | 1989–1990 Frequency of Observation[a] | 2008–2009 Frequency of Observation[b] |
|---|---|---|---|---|
| **Native** | | | | |
| *Adalia bipunctata* (L.) | 2-spotted | 1989 | common | rare |
| *Anatis labiculata* (Say) | 15-spotted | 1989 | occasional | not detected |
| *Brachiacantha ursina* (Fab.) | orange-spotted | 1989 | common | uncommon |
| *Coleomegilla maculata* (De Geer) | pink spotted | 1989 | common | common |
| *Chilocorus stigma* (Say) | twice-stabbed | 1989 | common | rare |
| *Coccinella novemnotata* Herbst | 9-spotted | 1989 | occasional | not detected |
| *C. trifaciata perplexa* Mulsant | three-banded | 1989 | occasional | rare |
| *Cycloneda munda* (Say) | polished | 1989 | common | uncommon |
| *Hippodamia glacialis* (Fab.) | — | 1994 | na | uncommon |
| *H. convergens* Guérin-Meneville | convergent | 1989 | common | rare |
| *H. parenthesis* (Say) | parenthesis | 1989 | common | rare |
| *H. tredecimpunctata tibialis* (Say) | 13-spotted | 1989 | occasional | not detected |
| *Hyperaspis undulata* (Say) | — | 1989 | occasional | not detected |
| **Exotic** | | | | |
| *Coccinella septempunctata* (L.) | 7-spotted | 1989 | common | common |
| *Harmonia axyridis* (Pallas) | multicolored Asian | 1994 | na | common |
| *Hippodamia variegata* (Goeze) | variegated | 2000 | na | uncommon |
| *Propylaea quatuordecimpunctata* (L.) | 14-spotted | 2006 | na | uncommon |

[a]From Maredia et al. 1992b. na = presumably not arrived yet.
[b]From LTER database. Common >5%, uncommon 1–5%, rare <1% of total captures.

two of the MCSE systems and found rarely in others. This is most striking for *Coleomegilla maculata* that is primarily found in corn, and for *H. convergens* that most commonly occurs in soybean. Other species like *C. septempunctata* and *Coccinella trifasciata perplexa* (Mulsant) are commonly found in multiple MCSE systems but only rarely in others.

### *Role of the Surrounding Landscape*

Coccinellids use various habitats in the landscape as they move from overwintering sites to spring and summer feeding habitats. By sampling native plant communities at the interface of woodlots and crop fields, Colunga-Garcia (1996) documented the role of early flowering plants such as spring beauty (*Claytonia virginica* L.) and common dandelion (*Taraxacum officinale* F.H. Wigg) in providing spring pollen sources to adult coccinellids emerging from overwintering sites. He also developed a model to estimate the location of overwintering sites based on the position of woodlots and early spring pollen sources.

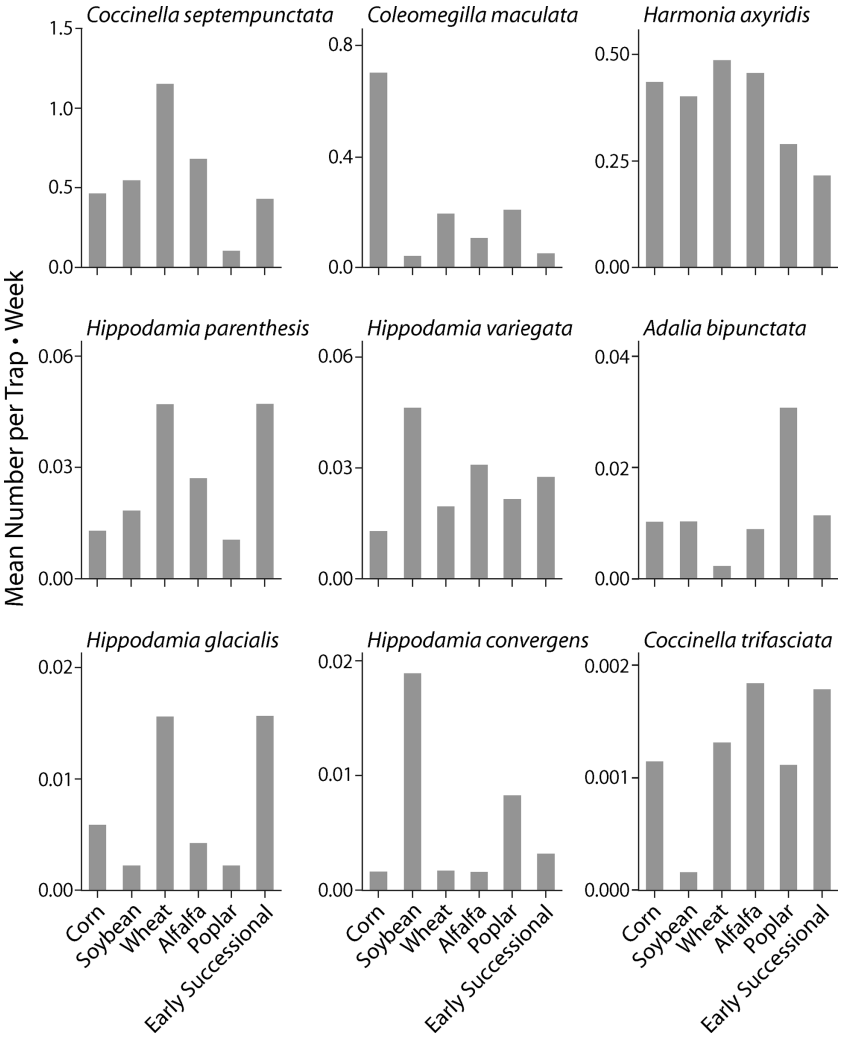


Figure 8.3. Summary of mean number of adults captured per weekly trapping interval for nine ladybird beetle species within different systems of the MCSE over 18 years (1989–2007). MCSE systems are described in Table 8.1.

Ostrom et al. (1997) used stable isotope techniques to show that the $\delta^{13}C$ and $\delta^{15}N$ ratios of coccinellids track those of their food sources and from this inferred patterns of coccinellid movement in the KBS landscape. In particular, they found that 32 and 68% of the diet of *C. maculata* were derived from alfalfa and corn pollen, respectively, which was consistent with the distribution of this species during their study. Subsequently, Colunga-Garcia et al. (1997) showed that the coccinellid community responded to overall landscape structure as measured by habitat diversity and patchiness. In concordance with prior studies, *C. maculata* was more abundant in a landscape that included corn, while *C. stigma* and

*Brachiacantha ursina* (Fab.) were more abundant in those that included deciduous forest habitats. Overall, coccinellid species richness increased in sites containing uncultivated habitats, demonstrating the importance of these habitats in shaping predator communities (Woltz and Landis 2014).

### *Documenting Invasive Species*

Long-term sampling at KBS has also been important for documenting the arrival of exotic coccinellids and their impacts on the predator community. When the MCSE was initiated in 1989, *C. septempunctata* was concluding its initial outbreak phase (Sirota 1990) and was the dominant coccinellid species. Subsequent observations show that this species exhibits roughly a 5-year population cycle (Fig. 8.4). In 1994 the KBS LTER trap network was the first to detect the occurrence of the exotic species *H. axyridis* in Michigan (Colunga-Garcia and Gage 1998) (Fig. 8.5). In contrast to *C. septempunctata*, which primarily inhabits field crops and herbaceous plants in old-field habitats, *H. axyridis* is considered a semi-arboreal species (Koch and Galvan 2008), inhabiting both trees and herbaceous habitats. These flexible habitat requirements allowed *H. axyridis* to become a dominant species in all MCSE habitats. Its occurrence in forested habitats was associated with a decline in the abundance of *B. ursina, Cycloneda munda* (Say), and *C. stigma*—all species that prefer wooded habitats—suggesting that competitive displacement may have been occurring. In 2005 another exotic coccinellid, *H. variegata*, was reported in Michigan for the first time at KBS and in three additional counties (Gardiner and Parsons 2005), although a subsequent search of KBS LTER records showed it was first detected in 2000. Finally, in 2006, the exotic 14-spotted lady beetle (*P. quatuordecimpunctata*) was discovered in Michigan (Gardiner et al. 2009a). This species

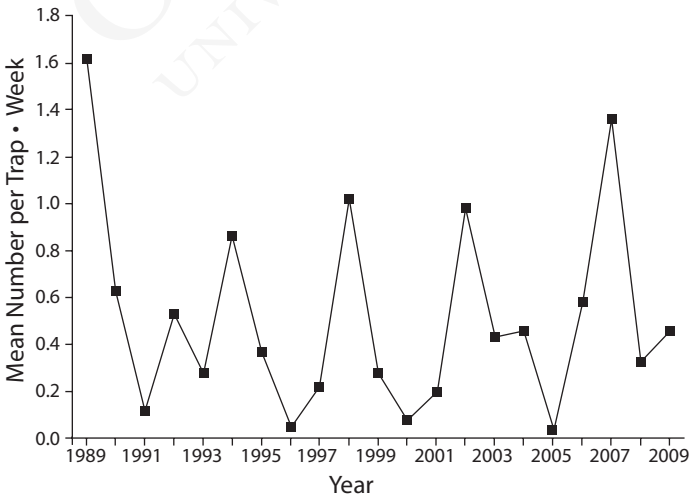


Figure 8.4. Mean number of *Coccinella septempunctata* ladybird beetle adults caught per trap over week-long deployments at the MCSE between 1989–2009.

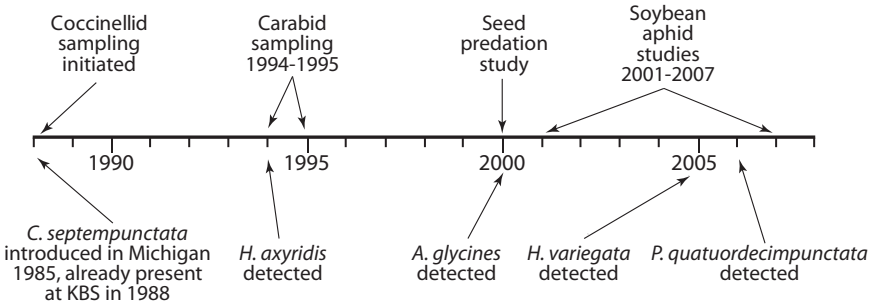


Figure 8.5. Time line showing insect sampling efforts (above line) and the arrival of key exotic coccinellid species (below line) to KBS LTER study sites. See Table 8.2 for full names of coccinellids; *A. glycines* is the soybean aphid *Aphis glycines*.

continued to increase and as early as 2008 was found to be the second most abundant coccinellid in corn after *C. maculata* (Gardiner et al. 2010).

Key lessons of these long-term coccinellid observations include a clearer understanding of the innate habitat preferences of different species (Fig. 8.3) and the seasonal movement of coccinellids from noncrop to crop habitats. As these predators move through the landscape (Isard and Gage 2001), they are influenced by the availability of prey and, as discussed below, can be important regulators of prey density. The addition of new exotic coccinellid species into the KBS landscape has shaped—and continues to shape—the structure and diversity of these communities (Bahlai et al. 2013, 2014).

## Soybean Aphid: A New Herbivore Changes Everything

The arrival of the soybean aphid *A. glycines*, an exotic invasive herbivore, into the KBS landscape created an opportunity to evaluate how a new link in the existing food web alters system dynamics. *A. glycines* is an invasive insect pest from Asia that was first discovered in the United States in 2000 and rapidly became the nation's most significant threat to soybean production (Ragsdale et al. 2004). Prior to its arrival, soybean experienced relatively low insect herbivore pressure and was seldom treated with insecticides. The arrival of the soybean aphid fundamentally changed soybean production, with the aphid becoming a key pest, frequently requiring insecticide applications to control (Ragsdale et al. 2011).

The soybean aphid overwinters as an egg on several species of shrubs/small trees in the genus *Rhamnus*, principally common buckthorn (*R. cathartica* L.), which is itself an exotic invasive pest. Several generations of *A. glycines* occur on buckthorn in the spring before alates (winged, sexually mature individuals) are produced and migrate to soybean. On soybean plants, females reproduce asexually (parthenogenesis) and give birth to live young, with multiple generations occurring on a single soybean plant. Soybean aphid populations can reach 30,000 aphids per plant (DiFonzo 2006, as cited in Walter and DiFonzo 2007) and result in yield losses of

up to 40% if left unchecked (Ragsdale et al. 2007). In September, alates are produced that return to *Rhamnus* spp., where mating occurs and eggs are laid.

Initial studies at KBS LTER and elsewhere found that *A. glycines* was attacked by a wide diversity of native and previously established predators (Fox et al. 2004, 2005; Rutledge et al. 2004) and parasitoids (Kaiser et al. 2007, Pike et al. 2007) with the potential to suppress *A. glycines* population growth. This provided the opportunity to ask several important questions:

(1) Is *A. glycines* primarily limited by top-down or bottom-up forces? Top-down forces represent the influence of higher trophic levels such as predation, whereas bottom-up forces represent the influence of lower trophic levels such as plant vigor or defense mechanisms.
(2) How do predators and parasitoids interact in the *A. glycines*–soybean system, and does intraguild predation (predation of potentially competing predators and parasitoids) alter the outcomes of these enemy interactions?
(3) Is predation/parasitism sufficient to cause a trophic cascade, whereby predators suppress herbivore prey, leading to increased crop yield?
(4) How does the occurrence of this new food source affect established coccinellid communities?
(5) How does landscape structure interact with enemy communities to alter *A. glycines* population dynamics?

Studies addressing these key questions were conducted at KBS as well as in commercial soybean fields in Michigan and throughout the U.S. North Central Region and are discussed below.

### *Top-Down vs. Bottom-Up Effects*

In a series of studies conducted in the MCSE, Costamagna and colleagues explored the impact of crop management and natural enemies on soybean aphid population dynamics (Costamagna and Landis 2006; Costamagna et al. 2007a, b). By contrasting soybean aphid population growth in the Conventional, No-till, and Biologically Based systems (Table 8.1), they were able to examine a full range of potential bottom-up influences (fertility, soil moisture, induced host defences, etc.) that could be generated under realistic soybean growing conditions. In addition, by excluding natural enemies from selected plots, Costamagna et al. contrasted the relative importance of top-down and bottom-up forces for keeping aphid populations in check. They found that predation reduced initial aphid establishment by ~30% in 24 hours and that, overall, top-down influences provided a 4- to 7-fold suppression of aphid populations (Fig. 8.6).

In contrast, these investigators found no evidence for significant bottom-up forces across the range of agricultural practices, that is, there were no agricultural practices that differed in their abilities to check aphid populations in the absence of predators. The natural enemy community at KBS is dominated by generalist predators (lady beetles, anthocorid bugs, syrphid fly larvae) and generalist aphid parasitoids (Braconidae). Coccinellids appear particularly important for controlling aphids, and intraguild predation—where predators attack other predators who are

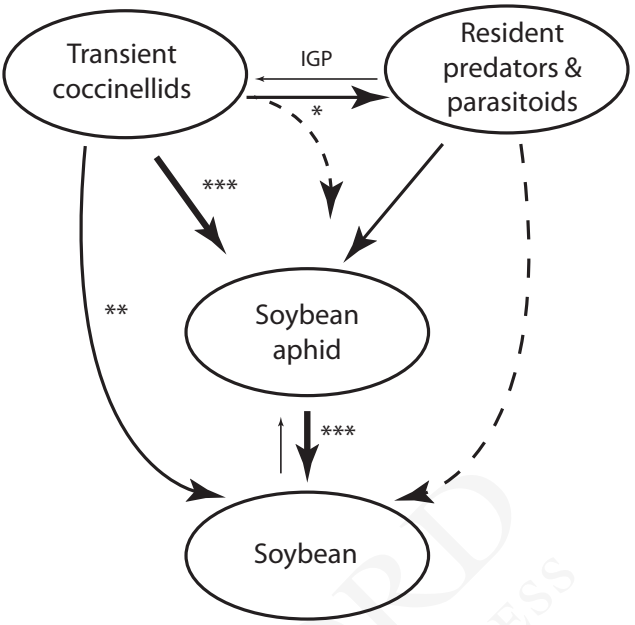


Figure 8.6. Summary of tri-trophic level interactions in the soybean aphid system. Thickness and direction of lines indicate the magnitude and direction of impacts. Dashed lines represent potential interactions that have not yet been shown to occur and asterisks represent increasing levels of statistical significance (P = 0.05 – 0.001). IGP = intraguild predation. Based on Costamagna and Landis (2006), Costamagna et al. (2007a, b, c; 2008), and Gardiner and Landis (2007).

their competitors—appears to be limiting the impacts of the parasitoid community (Costamagna and Landis 2006).

### *Intraguild Predation*

In subsequent studies conducted at the KBS LTER Biodiversity Gradient Experiment (Robertson and Hamilton 2015, Chapter 1 in this volume) and other locales, Costamagna et al. (2008) explored the role of intraguild predation between generalist predators and parasitoids. In addition, they examined the potential for the community of natural enemies to cause a trophic cascade (Costamagna et al. 2007a). They used selective exclusion cages that allowed the exploration of how the soybean aphid was impacted by parasitoids (in the absence of most predators) and by the presence of both predators and parasitoids. Results demonstrated the potential for season-long suppression of soybean aphid by the community of generalist natural enemies and a resulting trophic cascade, leading to increased soybean yield. In both studies, parasitoids alone provided statistically significant but biologically modest suppression of soybean aphid populations; they delayed peak aphid populations but not for long enough to suppress populations below their threshold for economic harm.

Predators attacked parasitoids (thereby demonstrating intraguild predation), but even when protected from predation, parasitoids were unable to provide economically significant levels of aphid control. In contrast, predators alone or in combination with parasitoids were capable of suppressing aphids below economic thresholds. Coccinellids were again identified as the key predators. These results support theoretical predictions that key predators can provide strong herbivore suppression even when they prey on species from other guilds within the natural enemy community (Costamagna et al. 2008).

### *Modeling Population Growth*

Modeling population dynamics can be a powerful tool for exploring scenarios that may be difficult to investigate empirically. While simple models frequently suffice, more complex species-specific models may be necessary to understand certain phenomena. Costamagna et al. (2007b) used the results of predator exclusion cage experiments at the KBS LTER and other sites to develop a series of models exploring soybean aphid population growth. Using a simple model, Costamagna and Landis (2006) estimated that in the absence of natural enemies the intrinsic rate of increase for *A. glycines* was very high ($r$ = 0.30–0.33), consistent with previous studies in other portions of the aphid's exotic range (Indonesia). Subsequently, Costamagna et al. (2007b) showed that *A. glycines* population growth could be more accurately simulated by incorporating an intrinsic rate of increase that declines linearly with time following soybean planting. They interpreted the decline in intrinsic growth rate as a response to declining host quality (i.e., older soybean plants may become less nutritious: a bottom-up control) that could interact with other mortality factors to play an important role in our understanding of overall aphid dynamics. For example, generalist natural enemies that continually suppress colonies of aphids may delay the growth of aphid colonies to a time when soybean growth is less suitable for their reproduction (Rutledge and O'Neil 2006). In this way, the early season impact of generalist predators becomes magnified by the later season impact of declining host quality. Finally, Matis et al. (2009) extended the specific model to more generally address the population dynamics of any organism specializing in the exploitation of ephemeral resources.

### *Field-Level Response to Soybean Aphid*

McKeown (2003) investigated the numerical response of the four dominant coccinellids in the KBS landscape (*H. axyridis, C. septempunctata, C. maculata, and C. munda*) to the presence of the soybean aphid and alternative prey at crop interfaces. Coccinellid predators were monitored for 18 weeks during the 2001 growing season in a field near the MCSE where corn and soybean were planted in alternated blocks (Fig. 8.7). Using an array of traps deployed within the two crops and at their interfaces, they showed that each of the four species displayed a marked preference for a particular habitat. Two species, *C. septempunctata* and *H. axyridis*, were significantly more likely to be found in soybean than in corn. In contrast, *C. maculata*, which is known to feed on corn pollen, exhibited an overwhelming preference

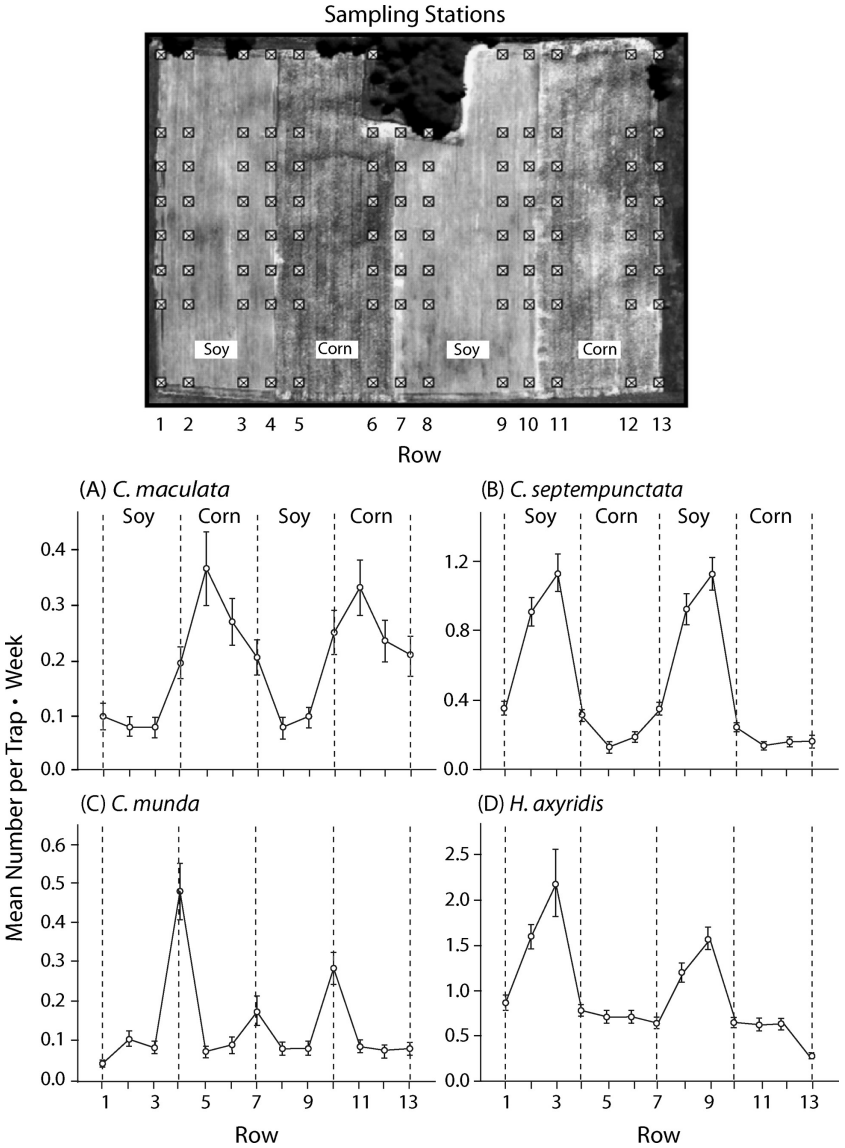


Figure 8.7. Average number of four coccinellid species captured per weekly trapping interval in soybean, corn, and interfacing areas within a large KBS field during 2001. A) *Coleomegilla maculata*, B) *Coccinella septempunctata*, C) *Cycloneda munda*, D) *Harmonia axyridis*. Aerial photo at top shows configuration of sampling stations. Figures indicate coccinellid abundance (mean ±SE)per crop habitat with rows 1, 4, 7, 10, and 13 representing edge habitats between crops; rows 2, 3, 8, and 9 habitats within soybean; and rows 5, 6, 11, and 12 habitats within corn.

for corn. Finally, *C. munda* was the only species that appeared to prefer the edge habitats. Within soybean where *A. glycines* was particularly abundant in 2001, only *C. septempunctata* and *H. axyridis* responded numerically to the presence of the aphid (McKeown 2003).

### *A Working Model of Pest Suppression*

Through many of the above observations, KBS LTER researchers have developed a working model of how soybean aphid suppression occurs. At the time soybean aphids first arrive in soybean fields, resident predators such as anthocorids and carabids—coupled with the feeding of more transient predators such as coccinellid adults—result in the elimination of some incipient aphid colonies, and more commonly the repeated suppression of those colonies that do establish. Sustained predation pressure, in conjunction with declining host suitability later in the season, can suppress aphid population growth. This effectively reduces food resources for the subsequent generation of natural enemies and may also reduce the numbers or fitness of aphids as they overwinter. Alternatively, if there are insufficient predators, or if aphid immigration overwhelms the predators' capacity to suppress their growth, aphid colonies will grow to the point that they themselves begin to produce alates and aphid abundance in the crop field may reach outbreak levels. Such aphid outbreaks provide a nearly unlimited food source for subsequent natural enemy generations and may increase natural enemy numbers (Fig. 8.8) and their overwintering fitness (Heimpel et al. 2010).

A useful analogy is to consider the incipient aphid colonies in a field as "spot fires" and generalist natural enemies as somewhat inefficient "firefighters." The firefighters continually find these spot fires and attempt to extinguish them. Sometimes they succeed in completely eliminating a colony, but more frequently, a few aphids are left behind. Under the right conditions, these "embers" may rekindle and allow the colony to persist and grow. If colonies reach sufficient size that they themselves begin to shed "sparks" (alate aphids), the field may soon become a "wildfire" (aphid outbreak) that the predators are unable to control. Alternatively, with sufficient numbers of predators, even if individually inefficient, a predator community may be able to keep aphid numbers low for an extended period of time. This holding action delays aphid population growth into the later season when conditions become less favorable for population outbreaks to occur.

### *Landscape Effects on Soybean Aphid Suppression*

The preceding analogy allows us to ask: What types of landscapes support a sufficient community of "firefighters" to result in effective soybean aphid suppression? Gardiner et al. (2009b) studied the impact of landscape structure on aphid-suppression services in soybean. In particular, they examined the community of mobile coccinellids that have repeatedly been shown vital to aphid suppression. Their studies demonstrate that these predators are responsive to landscape structure and that landscape diversity within 1.5 km of a soybean field is strongly related to the level of soybean aphid suppression. Landscapes with high proportions of land

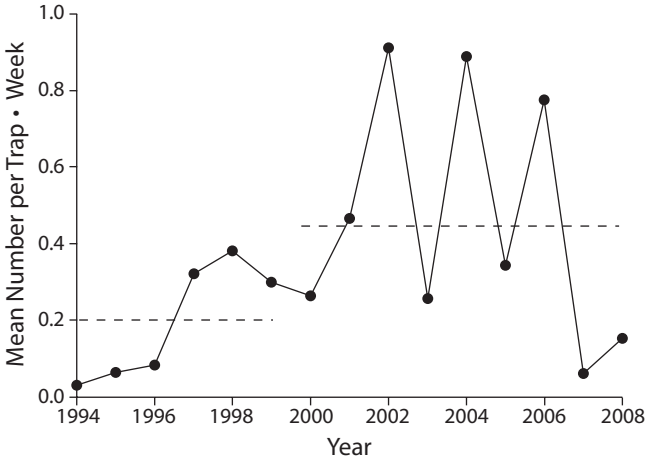


Figure 8.8. Mean number of *Harmonia axyridis* captured on yellow sticky card traps placed in multiple crop and non-crop habitats at the KBS LTER site, 1994–2008. Dotted lines show the mean numbers of *H. axyridis* from 1994 to 1999 (before soybean aphid arrival) and from 2000 to 2008 (after soybean aphid arrival). Note the response of *H. axyridis* following years of local *A. glycines* outbreaks (2001, 2003, 2005). Redrawn from Heimpel et al. (2010) with permission from Springer Science and Business Media.

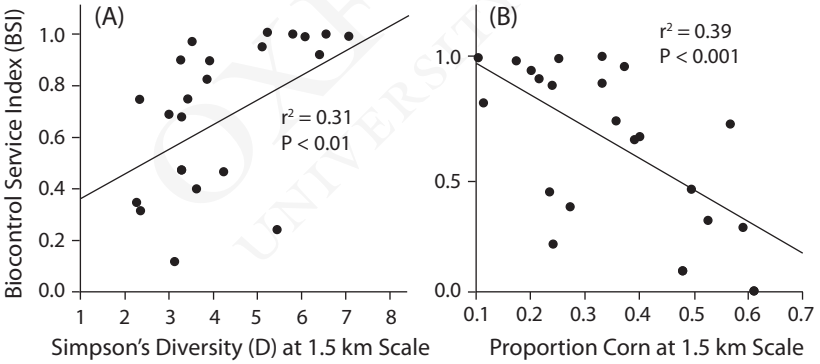


Figure 8.9. Biocontrol services from coccinellids as a function of landscape diversity (A) and the dominance of corn within 1.5 km of soybean fields (B). Panel (A) is redrawn from Gardiner et al. (2009b) with permission of the Ecological Society of America; permission conveyed through Copyright Clearance Center, Inc. Panel (B) is redrawn from Landis et al. (2008).

in corn production had low landscape diversity and significantly reduced biocontrol services in soybean fields (Fig. 8.9).

Landscape structure also altered coccinellid community structure, with the exotic *H. axyridis* more abundant in landscapes with patches of woody vegetation and native coccinellids more abundant in landscapes with abundant grasslands

(Gardiner et al. 2009a). An analysis of the value of biodiversity for aphid protection in these landscapes showed that for soybean producers using an integrated pest management strategy, natural suppression of aphids was worth ~\$33 $ha^{-1}$ in increased yield and decreased pesticide use in 2007, summing to >\$239 million $yr^{-1}$ for the four midwestern states studied (Landis et al. 2008).

KBS LTER research on soybean aphid–natural enemy interactions has yielded a number of key insights. First, results of observations and experiments support the hypothesis that communities of generalist natural enemies can provide effective herbivore suppression. At present, parasitoids are minor contributors to suppression in the soybean–aphid system, but could become more important with the importation of more effective parasitoid species (Wyckhuys et al. 2009), although intraguild predation could limit their effectiveness (Chacon et al. 2008). Second, soybean aphids serve as a food source and when abundant can support high coccinellid populations, particularly *H. axyridis*. This species, in turn, can act as an intraguild competitor, increasing its potential for negative impacts on native coccinellids (Colunga-Garcia and Gage 1998, Gardiner et al. 2011). Finally, based in part on data from KBS LTER, the soybean aphid system has been proposed as an example of "invasional meltdown" (*sensu* Ricciardi and MacIsaac 2000, Simberloff 2006), where the prior establishment of one exotic paves the way for others. Indeed, researchers investigating the soybean–soybean aphid system have documented such a cascade involving interactions among 11 Eurasian species (Heimpel et al. 2010).

## Summary

Twenty years of arthropod studies at KBS LTER have yielded insights that both confirm and extend ideas about basic ecology and the ecosystem services and disservices that arthropods contribute to agroecosystems. In particular, studies of arthropods at KBS have yielded insights relevant to basic population biology, food web ecology, and invasion biology theory. Studies of the soybean aphid have contributed to our understanding of top-down vs. bottom-up forces (Costamagna and Landis 2006); intraguild predation (Costamagna and Landis 2007, Gardiner and Landis 2007, Costamagna et al. 2008); trophic cascades in food webs (Costamagna et al. 2007a); and landscape control on herbivore–natural enemy interactions (Landis et al. 2008; Gardiner et al. 2009a, b). Population modelers have also used the soybean aphid system to elucidate a novel formulation of exponential growth based on cumulative density-dependent feedback (Costamagna et al. 2007, Matis et al. 2009). Moreover, they suggest key ways in which such systems may be designed to enhance desirable ecosystem services in the future.

One of the earliest and perhaps most fundamental lessons learned is that cropping systems form the proximate template on which pest and natural enemy interactions play out. The distribution of carabid beetles is sensitive to soil disturbance (e.g., till vs. no-till) and crop persistence (e.g., annual vs. perennial),

and this affects their potential importance as both insect and weed seed predators (Clark et al. 1997, Menalled et al. 2007). Similarly, some natural enemies appear to have innate preferences for specific crop types (e.g., *C. maculata* in corn), which influence their ability to provide predation services to other parts of the agricultural landscape. Spatial configuration of different crops within a local area also influences the distribution of insect predators, with coccinellids showing predictable patterns of movement from one crop to another throughout the season.

Taken as a whole, these findings suggest that at the farm scale growers have significant capabilities to manage their local landscape to promote more effective pest control services (Bianchi et al. 2006, Landis et al. 2000). However, landscape context also matters. Though landscape management is beyond the control of most farmers, except those with exceptionally large land holdings, it determines the regional pool of natural enemies that are present to move through individual fields (Gardiner et al. 2009a) and has critical implications for pest suppression (Gardiner et al. 2009b) and even crop profitability (Landis et al. 2008). Finally, the arrival of new exotic organisms has been a regular occurrence at KBS (Fig. 8.5) and has resulted in major shifts in plant productivity (Kosola et al. 2001), plant defense (Kosola et al. 2006), native insect communities (Colunga-Garcia and Gage 1998), and pest management (Costamagna and Landis 2006, 2007, Costamagna et al. 2007a, Costamagna et al. 2008).

Much remains to be learned about arthropod biodiversity and pest suppression in agricultural landscapes. Continuing studies at KBS LTER focus on understanding the role of transient generalist predators in regulating population levels of key herbivores (Woltz and Landis 2013) and the impact of landscape structure and keystone invaders such as *R. cathartica* in shaping these interactions. One of the most important forces poised to affect future agricultural landscapes is the creation of cellulosic biofuel cropping systems (Robertson et al. 2008). Future research at KBS LTER and elsewhere is needed to reveal how habitat type affects pest suppression services, and could provide a strong rationale for increasing landscape diversity via biofuel crop choice (Meehan et al. 2011).

In conclusion, arthropod predators and parasitoids play critical roles in regulating herbivore abundance and damage in agricultural systems. Likewise, there is evidence that arthropod seed predators may also influence weed population dynamics in row-crop systems. Work at KBS LTER has elucidated the relative influence of crop management and farm- and landscape-scale spatial heterogeneity on the ability of arthropod natural enemies to provide pest suppression services and thus reduce grower reliance on chemical pesticides. Case studies of carabid beetles, coccinellids, and soybean aphids illustrate a dynamic agricultural landscape where the arrival of exotic organisms—both herbivores and natural enemies—has had a major impact on insect dynamics and ecosystem performance. Moreover, they suggest that pest suppression services are influenced by features of both the crop production system and the broader landscape in which the crop is grown. Collectively, KBS LTER studies suggest that there is significant potential to understand and even design future agroecosystems to take better advantage of pest suppression services.

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