

The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring

Christine A. Bahlai · Manuel Colunga-Garcia ·
Stuart H. Gage · Douglas A. Landis

Received: 18 September 2013 / Accepted: 19 August 2014
© Springer International Publishing Switzerland 2014

Abstract Ladybeetles (Coleoptera: Coccinellidae) are ubiquitous predators which play an important role in suppressing pest insects. In North America, the coccinellid community is increasingly dominated by exotic species, and the abundance of some native species has declined dramatically since the 1980s. Several hypotheses have been proposed to describe the mechanism of invasion coupled with native species declines, e.g. vacant niche exploitation, intraguild predation, competitive exploitation and habitat compression. We analyze a 24-year dataset of coccinellid community structure in southwestern Michigan to elucidate the most likely mechanism(s) of native coccinellid decline and implications for their conservation. Correlation analyses indicated that impact of exotic species on native coccinellids varies with their degree of interaction. Although several native species

were observed to be in numerical decline, only *Adalia bipunctata* and *Coleomegilla maculata* had declines that were statistically significant. The magnitude of decline in these two species varied with the degree of dietary overlap with invaders, thus their decline is most likely driven by competitive exploitation. Habitat use patterns by some native species (*A. bipunctata* and *Coccinella trifasciata*) changed during years when the exotic *Harmonia axyridis* reached high numbers, lending support to the habitat compression hypothesis, where native species survive in ancestral (i.e. natural or semi-natural) habitats when invaders dominate cultivated habitats. Coccinellid communities occurring in semi-natural forested habitats were unique in both composition and variability from those occurring in cultivated habitats. Such semi-natural habitats can act as refuges for native coccinellids and may play a role in maintaining the functional resilience of coccinellid communities.

C. A. Bahlai (✉) · D. A. Landis
Department of Entomology, Center for Integrated Plant
Systems Lab, Room 204, Michigan State University, 578
Wilson Rd., East Lansing, MI 48824, USA
e-mail: cbahlai@msu.edu

M. Colunga-Garcia
Center for Global Change and Earth Observations, Room
205, Michigan State University, 1405 South Harrison
Road, East Lansing, MI 48823, USA

S. H. Gage
Department of Entomology, Michigan State University,
101 Manly Miles Building, 1405 South Harrison Road,
Lansing, MI 48824, USA

Keywords Ladybeetle · Ladybird · LTER ·
Community ecology · Invasive species · Exotic species

Introduction

Ladybeetles (Coleoptera: Coccinellidae) are a widely distributed and well-studied taxon. Due both to their distinctive and charismatic appearance, and their importance in suppressing herbivorous insects in a

variety of habitats, this taxon has been the subject of much research and public interest (Gardiner et al. 2012). In North America, coccinellid communities are increasingly dominated by exotic species, leading to concerns for native species which have dramatically declined in abundance in recent decades (Harmon et al. 2007). Exotic species frequently dominate the coccinellid community in disturbed agricultural habitats, but little is known regarding their impact on community structure (Snyder and Evans 2006). Specifically, it has been difficult to clearly demonstrate a causal relationship between exotic invasion and native species decline (Harmon et al. 2007; Kenis et al. 2009). For example, by 1985, at least 187 exotic coccinellid species had been intentionally or accidentally released in North America, and more than 26 species had become established (Gordon 1985). Initially many of these exotic species occurred at such low levels that they were rarely noted in surveys, and until 1985, 95 % of coccinellids reported in surveys in North America were native species (Harmon et al. 2007). However, since 1987, the percentage composition of native species has decreased to 67.5 %. Harmon et al. (2007) suggest that if exotic species were responsible for the decline in native coccinellids, either an ecological tipping point associated with the cumulative impact of the exotic species was reached in 1985–1987, or a particularly high impact species may have become established at or around this time.

There are four hypotheses that may explain the success of exotic coccinellid species and their potential impact on native species. (1) Vacant niche. Under this scenario, the presence of a previously vacant niche, such as a particular prey item that was not exploited by native coccinellids, is invaded by an exotic coccinellid species. Because the exotic species would not be competing with the native species for food resources, this would decrease net prey abundance within the landscape but would not affect densities of native species (Harmon et al. 2007; Snyder 2009). (2) Intraguild predation. An invading exotic species may engage in this form of interference competition, where the exotic species consumes native coccinellids as well as aphid prey. This scenario could result in decreased abundance of native coccinellids (Cottrell 2005; Hautier et al. 2011; Kajita et al. 2010; Michaud 2002; Raak-van den Berg et al. 2012; Reitz and Trumble 2002; Takizawa and Snyder 2012), and could potentially disrupt biological control of shared

prey, leading to a net increase in prey abundance (Rosenheim et al. 1995). (3) Competitive exploitation. If the exotic coccinellids are more effective at surviving in the environment or obtaining resources than the native species, the exotic species will competitively displace native species already occupying certain niches via exploitation. Because the exotic species is able to acquire resources more effectively than the native species, this would result in a net decrease of prey density and a decline in the density of native coccinellids (Harmon et al. 2007; Snyder 2009). (4) Habitat compression. As a consequence of competitive exploitation by exotic species in formerly resource-rich habitats, native species may change their patterns of habitat use. In this scenario, the native species would be observed in lower numbers in habitats that are well-exploited by exotic species, and would be ‘compressed’ to habitats where exotics do not thrive (Alyokhin and Sewell 2004; Evans 2000, 2004; Evans et al. 2011).

The literature support for these four hypotheses is variable and sometimes conflicting. The vacant niche hypothesis has been largely dismissed because of the observed widespread declines of native species, suggesting that competitive interactions are indeed occurring between exotic and native species. The intraguild predation hypothesis has garnered more empirical support. In fact, numerous studies have shown that several key exotic coccinellids are more likely to perpetrate intraguild predation than be victims of it (Cottrell 2005; Foley et al. 2003; Hautier et al. 2011; Kajita et al. 2010; Michaud 2002; Raak-van den Berg et al. 2012; Takizawa and Snyder 2012). However, there is little evidence that intraguild predation is driving the decline of native coccinellids in field studies (Snyder 2009). The amount of intraguild predation detected does not vary with the relative abundance of exotic coccinellids, and several studies have concluded that exotic species do not contribute disproportionately to intraguild predation compared to native species under field conditions (Gagnon et al. 2011; Gardiner et al. 2011; Smith and Gardiner 2013; van de Koppel et al. 1997). The competitive exploitation hypothesis appears to be the most supported by the available data according to Harmon et al. (2007). Competitive exploitation and subsequent displacement of native species most commonly occurs when the exotics and natives competing for the same resources are closely related (i.e. within the same

sub-family, as with most aphidophagous coccinellids). This form of competition can occur via several mechanisms, such as comparatively enhanced foraging ability or reduced susceptibility to diseases or natural enemies, and at a variety of temporal and spatial scales (Reitz and Trumble 2002). Impacts of biological invasions on native communities are often mitigated by spatial or temporal circumstances, e.g. species might occupy mutually exclusive habitats or survive in refuge habitats where exotics do not dominate (Hesler and Kieckhefer 2008; Krassoi et al. 2008). The habitat compression hypothesis, actually proposed within the framework of the competitive exploitation hypothesis, predicts that native species will survive in greater proportions in ‘ancestral’ (i.e. natural and semi-natural) habitats upon the arrival of an invader (Evans 2000, 2004; Evans et al. 2011; Finlayson et al. 2008). Under this hypothesis, agricultural crops are seen as introduced habitats that may have provided an opportunistic expansion in habitat range for North American native coccinellids. These native species were able to exploit those relatively newly created niches in the absence of competition, and may have even come to prefer them over ancestral habitats. However, when Eurasian species with a longer history of specialization in crop habitats were introduced, the adventive niches were no longer open for opportunistic native species. Native coccinellids survived primarily in their ancestral habitats in a phenomenon denominated habitat compression. Because these niche habitats are fewer now than before European settlement of North America, the landscape supports fewer native coccinellids (Acorn 2007).

While an understanding of the mechanisms of exotic coccinellid invasion and its implications for native coccinellid decline is needed, there are multiple challenges in testing these hypotheses. Coccinellid communities occurring in both natural and agricultural landscapes are usually dominated by two to four species at any one time (Bahlai et al. 2013; Hodek and Honek 1996). Additionally, coccinellid assemblages typically undergo dramatic variability in diversity and overall abundance from year to year, making it very difficult to discern the impact of exotics on the community over the duration of a typical study (Elliott et al. 1996). Causes of this variability are poorly understood, but may be related to population dynamics of individual species or variability in environmental conditions. The

composition of coccinellid communities also varies from location to location (Gordon 1985), thus if the degree and type of interaction are species specific, mechanisms of interaction may not be generalizable. Finally, coccinellids are highly mobile predators and often move between habitats when foraging (Woltz and Landis 2013). This makes it very challenging to discern whether individuals are residing in a particular habitat or just moving through the landscape (Ostrom et al. 1996). Thus, a highly systematic approach and large number of observations are required before trends can be detected. Here, we evaluate a 24-year dataset documenting the abundance of nine native and four exotic species of coccinellid occurring in nine plant habitats in an agricultural landscape in southwestern Michigan. We look for evidence supporting or refuting the proposed hypotheses to explain the observed decline of native coccinellids.

Methods

This study analyzes an existing dataset documenting the abundance of aphidophagous coccinellids collected at Michigan State University’s Kellogg Biological Station (KBS) in southwestern Michigan (42°24’N, 85°24’W) (Maredia et al. 1992a). Data collection started in 1989 at the KBS Long Term Ecological Research (LTER) site as part of the Main Cropping System Experiment (MCSE) and associated forest sites, and continues to date. The subset of data examined for this study spanned 1989–2012. Data and associated pre-processing and sub-setting methods are additionally detailed in Bahlai et al. (2013).

Description of study site and classification of habitats

The MCSE consisted of treatments of annual field crops (maize, soybeans and wheat) in rotation, as well as alfalfa, hybrid (biomass) poplar and herbaceous early successional vegetation. Each treatment was replicated six times with individual plot sizes of 1 ha. Observations were taken from five permanent sampling stations within each plot. Forest sampling began in 1993, at sites within 3 km of the MCSE on the KBS. Forest types included: 40–60 year old conifer forest plantations, late successional deciduous forest, and successional forests occurring on abandoned

Table 1 Site agronomic history

Habitat	CF*	DF	SF	ES	Poplar	Alfalfa	Soybean	Wheat	Maize	Notes
1989										
1990										Poplar aphid outbreak
1991										
1992										
1993										
1994										
1995										
1996										
1997										ES plots burned in April
1998										
1999										
2000										Rye was planted instead of alfalfa
2001										Soybean aphid detection in region
2002										Soybean aphid outbreak in region
2003										ES plots burned in May
2004										ES plots burned in April
2005										Soybean aphid outbreak in region
2006										ES plots burned in April
2007										
2008										ES plots burned in April
2009										ES plots burned in March
2010										Poplar replanted
2011										ES plots burned in March
2012										ES plots burned in April

Shaded areas indicate crops that were planted or growing at the Kellogg Biological Station LTER site and monitored for coccinellids in a given year. CF coniferous forest, DF deciduous forest, SF successional forest, ES early successional fields

agricultural land. Three 1 ha replicates of each forest type were monitored at five sampling stations, as in the MCSE. Pertinent agronomic records for the site are summarized in Table 1 and detailed records are available at <http://lter.kbs.msu.edu/datatables/150>. Coccinellid abundance data for the duration of the study is available online at <http://lter.kbs.msu.edu/datatables/67>. A relational database in MS Access® integrating coccinellid data with relevant environmental and agronomic records to facilitate analysis is available from the authors by request.

Adult coccinellids were monitored using un-baited two sided yellow cardboard sticky cards (Pherocon, Zoecon, Palo Alto, CA, USA) suspended 1.2 m above the ground at each sampling station (Bahlai et al. 2013; Maredia et al. 1992a). Each week, coccinellids on the sticky cards were identified and recorded. The length of the sampling period within the growing season

averaged 14 weeks, but varied between 8 and 22 weeks depending on the availability of labor, crop type and environmental conditions. Although sticky cards are imperfect estimators of coccinellid density (Musser et al. 2004) and may vary in efficiency between habitats (Bahlai et al. 2013), this method provided us with an inexpensive sampling tool that could be consistently deployed in the long term. Because of these biases, we emphasized within-habitat changes in abundance in our analyses.

Data pre-processing

The relative abundance of 13 species of aphidophagous coccinellids was used in the analysis. Species included in the analysis were the natives *Adalia bipunctata*, *Coleomegilla maculata*, *Chilocorus stigma*, *Coccinella trifasciata*, *Cycloneda munda*,

Hippodamia tredecimpunctata, *Hippodamia convergens*, *Hippodamia glacialis*, *Hippodamia parenthesis*, and the exotics *Coccinella septempunctata*, *Harmonia axyridis*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata*. The European species, *C. septempunctata* (Hodek, Michaud 2008), was first detected at the site in 1985; *H. axyridis*, an Asian species (Koch 2003), was first detected in 1994; *H. variegata*, a Eurasian species (Gordon 1987), was first detected in 1999; and *P. quatuordecimpunctata*, a European species (Dysart 1988), was first detected in 2007.

For analyses and data presentation, individual habitats were grouped into three habitat types: annual crops, perennial crops, and forest habitats. Annual crops were all dominated by annual herbaceous plants, in near monoculture, and included maize, wheat, and soybeans, while perennial crops included poplar, alfalfa, and managed early successional. Managed early successional habitat was also included as a perennial 'crop' because it is a community resulting from abandoned crop land, occurring within a crop matrix, and managed to maintain its successional stage through yearly burnings. Finally, forest habitats included coniferous, deciduous, and successional forest.

Data were examined at two different temporal resolutions to gain insight into both real-time interactions and between season trends. First, the sum of all captures from each sampling station in a given week, in a given treatment by replicate combination, was called 'weekly average,' and the sum of all captures in a given treatment over a calendar year, was referred to as 'yearly total.' To reduce the likelihood of erroneous conclusions from a large dataset with numerous sources of environmental variation, $\alpha = 0.01$ was observed for all analyses. All statistical analyses excluded data collected prior to 1993, when the forest habitats began to be monitored. Data collected prior to this date were used in descriptive analyses only.

During 2000–2006 there were repeated outbreaks of soybean aphid (*Aphis glycines*) in the study area which represented a major change to the aphid resource structure available to coccinellids (Heimpel et al. 2010; Knapp et al. 2012). Thus, for several analyses, data were grouped into three phases by observation year: from the initiation of the study to 1999 (pre-soybean aphid, phase A); from 2000–2006 (soybean aphid outbreak years, phase B); and 2007–2012 (soybean aphid present, but not at outbreak

levels, phase C). These groupings are hereafter referred to as aphid resource structure phases.

Data analysis

To visualize trends in the abundance, population dynamics and habitat use patterns of each coccinellid species over time, time series of captures per trap per year were plotted for each of the habitat types. To determine if communities of coccinellids differed by habitat type, the data were fourth root transformed and then Bray–Curtis similarities between all coccinellid species by habitat at the yearly resolution were subjected to non-metric multidimensional scaling (NMDS) in PRIMER 6.1.13 (Clarke and Gorley 2006). Community composition was compared using analysis of similarities (ANOSIM), a distribution-free method for comparing groupings in multivariate data, and community variability was compared using the distance based test for homogeneity (PERMDISP), a permutational analysis of multivariate dispersions (Clarke and Gorley 2006). Habitat use patterns by individual coccinellid species by year were also subjected to non-metric multi-dimensional scaling in PRIMER to detect changes in habitat use over time. Data were fourth root transformed, and Bray–Curtis similarities of captures per trap per habitat type were subjected to NMDS and then ANOSIM was used to compare habitat use patterns of each species relative to resource structure phase. If habitat use changes were detected, similarity percentage analysis (SIMPER) was performed to determine how habitat use changed (Clarke and Gorley 2006). *H. variegata* and *P. quatuordecimpunctata* were excluded from these analyses because they are relatively recent additions to the community and thus inadequate data existed to explore temporal patterns in their habitat use. Spearman rank correlations were computed for each species combination, both across all habitats and within habitat groupings, for both temporal resolutions to detect interactions between species using the package Hmisc in R 2.15.1 (Harrell Jr and Dupont 2013; R Development Core Team 2012). Spearman rank correlations were also computed for each species-habitat and species-environmental-temporal variable combination to detect interactions between individual species and abiotic or habitat conditions. Categorical variables (habitats) were encoded as binomial variables for analysis.

Results

Population time series

Overall abundance of coccinellids was widely variable over the duration of the study in all three habitat types (Fig. 1a). The native species *A. bipunctata* (Fig. 1b) rapidly decreased in abundance in the early 1990s. This species was observed only in annual and perennial crops until 1999, and then exhibited a shift in habitat use, occurring only in forest habitats from 2002 to 2012. *C. maculata* (Fig. 1c) maintained relatively constant abundance over the course of the study within annual cropping systems. In annual crops, this species underwent a 3 year cycle of abundance, likely related to crop rotation, as it was typically more abundant in years when maize was planted at the site (Table 1). *C. maculata* was relatively common in perennial crops early in the study, but was only rarely observed in perennial or forest habitats after 1993. *C. stigma* (Fig. 1d) occurred at low levels, undergoing apparently stochastic dynamics in all habitats, although there are several gaps in the records for this species in annual crops. *C. trifasciata* (Fig. 1e) was at very low density in general, but maintained a 2–3 year cyclical abundance, alternating between perennial and annual habitats for most of the duration of the study. In 2001 and 2002, this species exhibited a shift in habitat use, occurring for the first time in forest habitats, while simultaneously appearing at lower-than-usual numbers in annual crops, and disappearing from perennial crops altogether. In 2005, *C. trifasciata* was once again observed in perennial and annual crops, but was not observed in any habitat from 2010 to 2012. *C. munda* (Fig. 1f) was a relatively common species which occurred at moderate levels in perennial habitats from 1989 to 2000 but declined in this habitat after 2003, and has since been recorded in all habitats at variable levels. *H. convergens* (Fig. 1g) occurred at the site at very low densities for the duration of the study, with a spike in abundance in annual crops in 1997. No records for this species exist for 2004–2008. *H. glacialis* (Fig. 1h) occurred at very low densities at the outset of the study but increased in all habitats throughout the later 1990s, and had spikes in activity in annual and perennial habitats in 2004–2005, and 2008–2010. *H. parenthesis* (Fig. 1i) was also present at very low densities, but seemed to undergo a 2–3 year cycle of abundance in all habitats, with a

Fig. 1 Average trap captures per year of thirteen species of coccinellid at Kellogg Biological station, Hickory Corners, MI, 1989–2012. Each panel documents time series of average captures in the annual (circles, solid lines) and perennial (points, dotted lines) crop habitats and in the adjacent forest habitat (triangles, dashed lines). **a** Total captures, all aphidophagous coccinellids; **b** *A. bipunctata* ABIPN; **c** *C. maculata* CMAC; **d** *C. stigma* CSTIG; **e** *C. trifasciata* CTRIF; **f** *C. munda* CMUND; **g** *H. convergens* HCONV; **h** *H. glacialis* HGLAC; **i** *H. parenthesis* HPARN; **j** *H. tredecimpunctata* HTRE; **k** *C. septempunctata* CSEPT; **l** *H. axyridis* HAXY; **m** *H. variegata* HVAR; **n** *P. quatuordecimpunctata* PQUA. Dark arrows in panels **b** and **e** indicate an apparent change in habitat use. Panel **a** of this figure originally appeared in Bahlai et al. (2013). Note differenced in y-axis scales between panels

period of lower abundance in 2002–2006. *H. tredecimpunctata* (Fig. 1j) occurred at the site at very low densities, with a small spike in abundance in annual crops in 2000. After 2000, it declined in abundance and was last observed at the site in 2003. No records for this species exist beyond 2004.

Exotic species, in general, were more abundant than native species. *C. septempunctata* (Fig. 1k) occurred in high numbers from the beginning of the study. It was abundant in annual and perennial crops, and rare in forest habitats. In annual crops, this species exhibited a consistent 4–5 year cycle in abundance that appears unrelated to crop rotation or prey availability. *H. axyridis* (Fig. 1l) was first captured in 1994, and steadily increased in all habitats until 2001. Then, this species exhibited a 2-year cyclical abundance in annual and perennial crops until 2006, related to the arrival of soybean aphid (*A. glycines*) to North America (Rhainds et al. 2010), and uniformly decreased in abundance in forest habitats after 2003. *H. variegata* (Fig. 1m) was first detected at the site in 1999 and has occurred at variable, low levels in annual and perennial crops since. Although the duration of observation period for this species was relatively short compared to species present since the initiation of the study, a 3–4 year boom bust population cycle appears to be emerging for this species. *P. quatuordecimpunctata* (Fig. 1n) was first observed in 2007, and appeared to be increasing in density in both annual and perennial crops.

Species interactions

Non-metric multidimensional scaling suggested that coccinellid communities differed in both composition

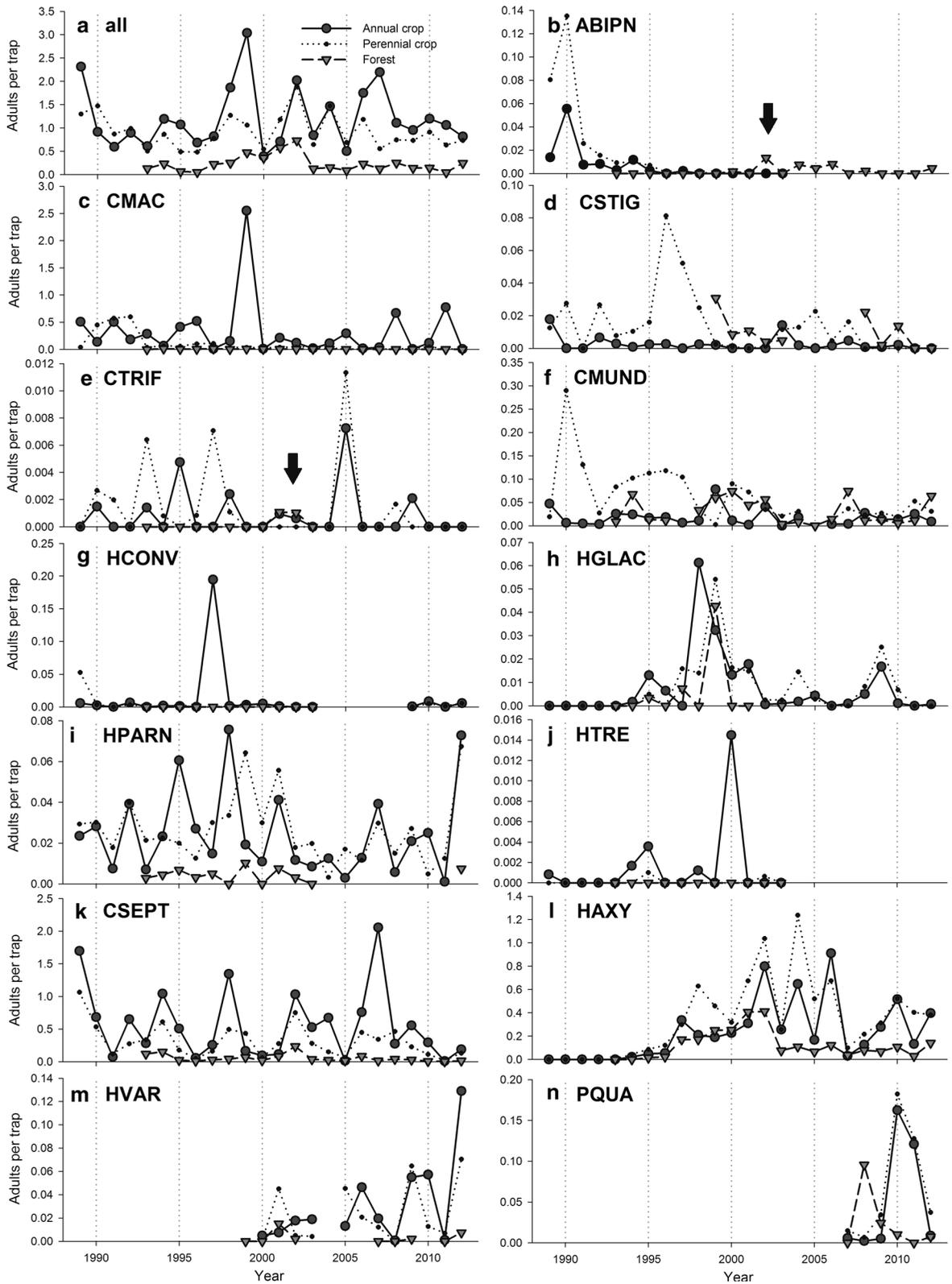
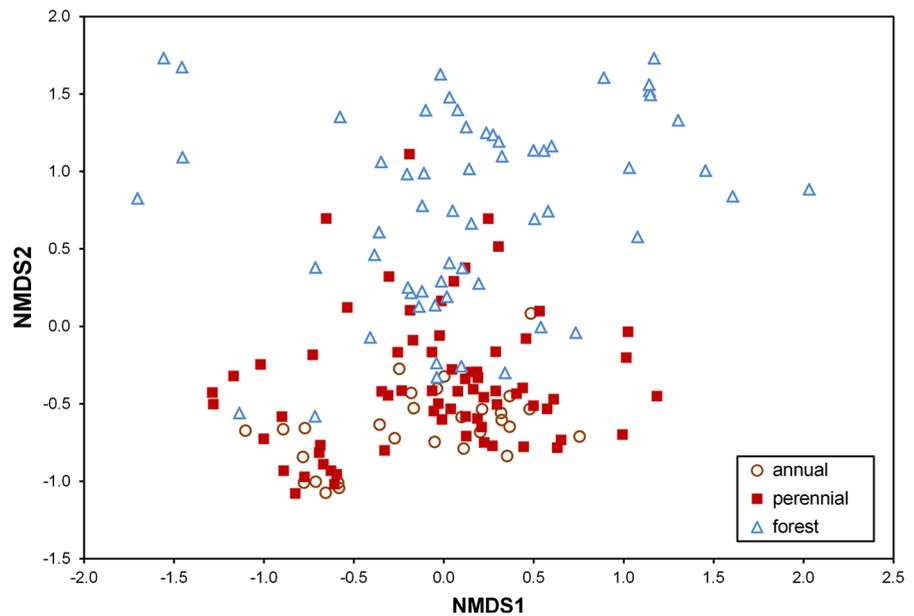


Fig. 2 NMDS of coccinellid captures by habitat type for thirteen species of coccinellid at Kellogg Biological station, Hickory Corners, MI, 1993–2012. Distances in figure represent Bray–Curtis similarity of fourth root transformed coccinellid captures by year and habitat type



and variability between crops and forest (Fig. 2). Community composition differed by habitat, as did dispersion of communities (ANOSIM: Global $R = 0.295$, $p = 0.001$; PERMDISP: $F_{2,155} = 13.98$, $p = 0.001$), and although communities occurring in annual and perennial habitats did not differ, and, in fact, overlapped substantially, both differed significantly from forest communities in both composition and dispersion (annual vs. forest, ANOSIM: $R = 0.406$, $p = 0.001$; PERMDISP: $t = 4.44$, $p = 0.001$; perennial vs. forest, ANOSIM: $R = 0.390$, $p = 0.001$; PERMDISP: $t = 3.98$, $p = 0.001$).

The habitat use patterns of individual species did not vary by resource structure phase (Fig. 3), but for one exception. The habitat use of *A. bipunctata* changed significantly after the arrival of soybean aphid (Fig. 3a; ANOSIM: Global $R = 0.678$, $p = 0.003$), and 100 % of this change can be attributed to the shift from perennial and annual crops into forest habitats at this time (SIMPER; average dissimilarity = 100 % between phases A and B, A and C; 10.5 % dissimilarity between B and C). Despite the observed habitat shift in the time series, the habitat shift observed for *C. trifasciata* was not statistically significant (Fig. 3d). This is likely because the shift was both slight and temporary; the 2 years where the effect occurred (2001 and 2002) cluster differently than the rest of the values, and very similarly to each

other (Fig. 3d). Finally, *H. glacialis* and *H. parenthe-sis* habitat use patterns clustered strikingly (Fig. 3g, h), but these patterns appear to be more related to rotation of annual crops than to aphid resource structure phase.

Species correlations at both temporal resolutions (weekly and yearly) are summarized in Fig. 4. Numerical values of Spearman's ρ for species–species correlations based on weekly and yearly data resolutions across the site and within habitat types are given in Appendix Tables 2 and 3, respectively. Positive correlations were more common than negative ones (Fig. 4). The only strongly negative correlation within the weekly data was between *H. axyridis* and *A. bipunctata* ($\rho = -0.18$), although *H. axyridis* was also moderately negatively correlated with *C. maculata* ($\rho = -0.08$, Fig. 4a). The strength of relationship observed varied between habitats; for instance, *A. bipunctata* was moderately negatively correlated with *H. axyridis* in annual ($\rho = -0.21$) and perennial habitats ($\rho = -0.20$), but not in forest habitats (Appendix Table 2). All the non-native species were positively correlated with each other, but the magnitude of the correlation varied: *H. axyridis* was strongly positively correlated with *H. variegata* ($\rho = 0.22$), moderately correlated with *P. quatuordecimpunctata* ($\rho = 0.15$), and only slightly positively correlated with *C. septempunctata* ($\rho = 0.07$, Fig. 4a).

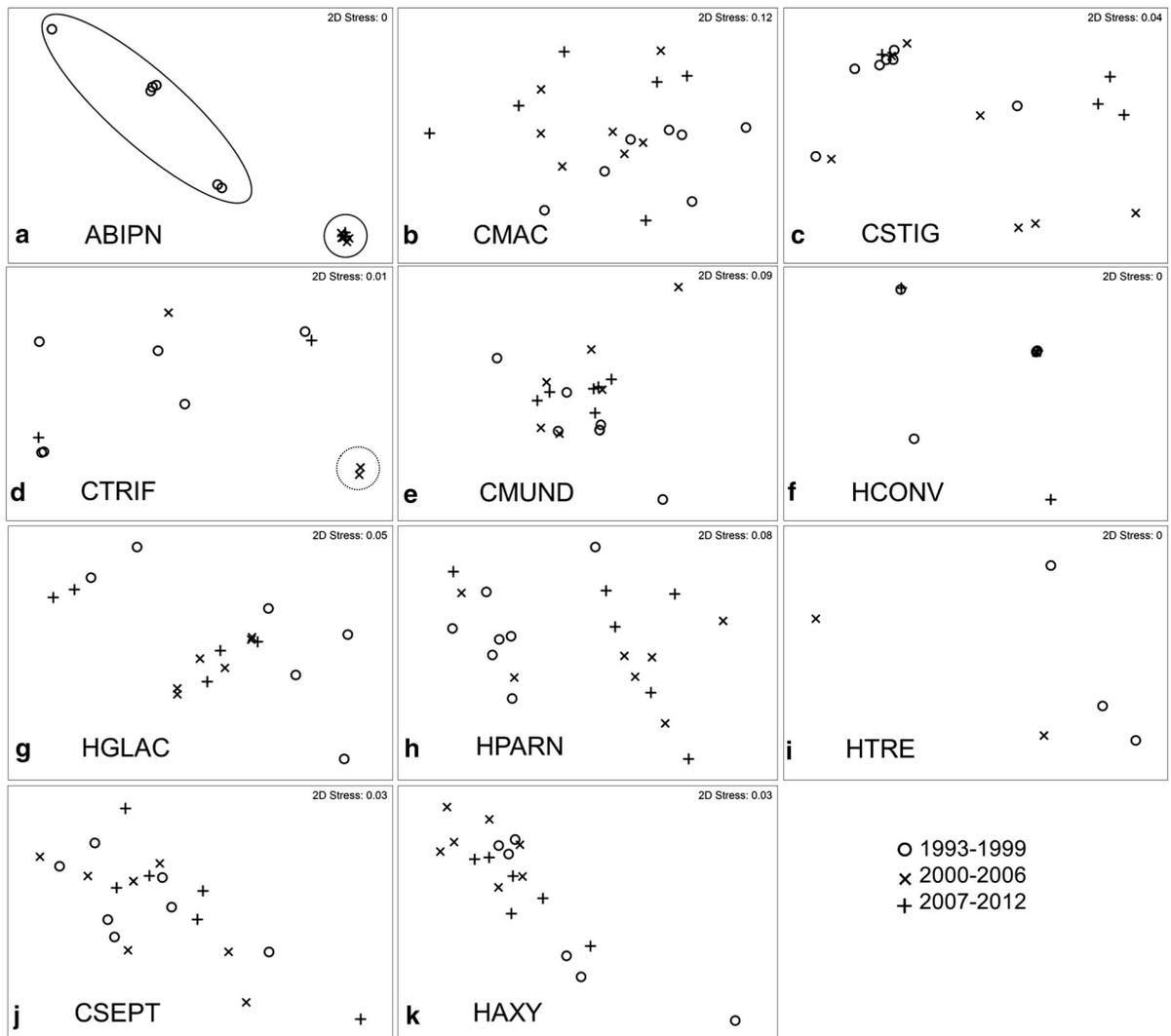


Fig. 3 NMDS of coccinellid captures in three habitat types, by species, for eleven species of coccinellid at Kellogg Biological Station, Hickory Corners, MI, 1993–2012. Distances in figure represent Bray–Curtis similarity of fourth root transformed coccinellid captures by year and habitat type. Each panel represents habitat use for an individual species. Symbols

correspond to phases in aphid resource structure (see “Methods”). Species abbreviations are as used in Fig. 1. Solid ellipses in panel a demarcate statistically different groupings. Dashed ellipse in panel d demarcate a temporary shift in habitat use observed within time series data

Within the yearly dataset (Fig. 4b), *A. bipunctata* was negatively correlated with all non-native species except for *C. septempunctata*. As was observed at the weekly data resolution, the negative correlation was strongest between *A. bipunctata* and *H. axyridis* in annual and perennial crops ($\rho = -0.78$ and $\rho = -0.74$, respectively), and no relationship was observed in forest habitats (Appendix Table 3). *H. axyridis* was only positively correlated with the non-

native *H. variegata* ($\rho = -0.18$), and the native *H. glacialis* ($\rho = -0.18$), at this resolution, although *C. septempunctata* was positively correlated with four native species in this analysis (Fig. 4b). Interestingly, *C. septempunctata* had a slight negative relationship with one of these species, *C. stigma* ($\rho = -0.05$), at the weekly resolution (Fig. 4b).

Species-environment and species-habitat correlations at both temporal resolutions (Spearman’s ρ) for

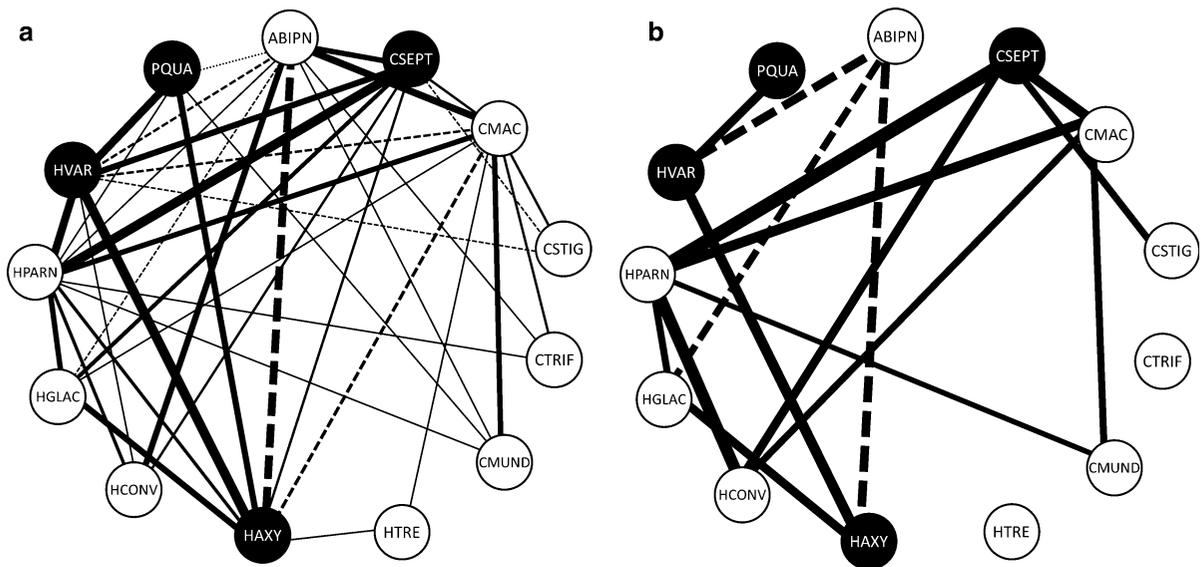


Fig. 4 Relative correlation between 13 species of coccinellid at Kellogg Biological Station, Hickory Corners, MI, 1989–2012, based on Spearman's ρ ($p < 0.01$) on site-wide abundance data at **a** weekly and **b** yearly resolutions. Line widths represent Spearman's ρ values within a given resolution, but are not to

scale between analyses at the two resolutions. Solid and dashed lines indicate positive and negative correlation respectively. Species abbreviations are as used in Fig. 1. Shaded circles indicate exotic species. Complete correlation analysis results are provided in the Appendix Tables 2 and 3

all statistically significant correlations at both data resolutions are provided in Appendix Table 4. Day of year, degree day accumulation, and mean temperature had low to moderate correlation with many species (Table 4), but total degree day accumulation for the year was uncorrelated with abundance of any species of coccinellid, and mean temperature over the sampling period was moderately correlated with only two species at the yearly resolution (Table 4). Weekly total precipitation was only weakly correlated with three species (Table 4), and yearly total precipitation was not correlated with the abundance of any species. Three of the thirteen monitored species were positively correlated with year, while two species were negatively correlated with year (Table 4). Species that increased with year included the three exotic species arriving during the course of this study, *H. axyridis*, *H. variegata*, and *P. quatuordecimpunctata*. Species that were negatively correlated included *A. bipunctata* and *C. maculata*, both native species that were relatively dominant in the aphidophagous coccinellid community at the study site at the outset of the study.

Species-habitat type correlations were widely variable, and within the weekly data, most combinations were significant, even if correlation was weak (Table 4). Yearly comparisons were only significant if

the relationship was considerably stronger. Within the yearly dataset, no significant habitat correlations were observed for *A. bipunctata*, *C. trifasciata*, *H. axyridis*, *H. variegata* or *P. quatuordecimpunctata* (Table 4). Five species were negatively correlated with forest habitat. Species that were positively correlated with annual crop habitats were mutually exclusive from species correlated with perennial habitats.

Discussion

Status of native coccinellids

The coccinellid community in southwestern Michigan has become increasingly dominated by exotic species. Although still dramatically variable in composition from year-to-year, when examined in aggregate, in the first 5 years of this study combined, native species represented nearly one half of all coccinellids captured, while in the latter 5 years, only 28 % of captures were native species (Bahlai et al. 2013). Within our analysis, the bulk of native species decline could be explained by decreased abundance of *C. maculata* and *A. bipunctata* (Table 4). No other declines of native species were statistically detectable during the analyzed period. This

result is somewhat surprising. In previous studies, *H. axyridis* was implicated in the declines observed in many non-dominant native species at this site immediately following its arrival (Colunga-Garcia and Gage 1998). Yet, these declines have since stabilized or reversed and are no longer statistically detectable (Fig. 1; Table 4). This suggests that responses of coccinellid species to invasion are idiosyncratic, and temporary declines with subsequent recovery are possible.

Our sampling methodology was limited in its ability to detect certain species of coccinellid, particularly those occurring in arboreal habitats. Traps were held 1.5 m above ground across all habitats to maintain consistency. However, it is likely that the much of the coccinellid activity within our forest plots occurred within the tree canopy. Because we were unable to detect certain species known to be extant at the site with our sampling methodology (e.g. arboreal species such as *Anatis mali*), the status of these species is unknown. It is also likely that overall density of all species observed occurring in the forest plots was systematically underestimated due to this sampling bias.

Although no records of *H. tredecimpunctata* exist beyond 2004, species still continues to occur at our site at very low levels, but was not detected later in our study period due to a sampling error. Because this species is extremely rare (captures of ca. 1 individual per year), it appears to have been omitted from the data sheets where field data was recorded from 2004 to 2013, and thus records do not exist in our database for this time period. Since rectifying this error in the 2014 sampling season, we have captured an individual of this species within the poplar treatment (CB, unpublished data).

Persistence of exotic species

Our results suggested that, unlike the three exotic species that arrived to the site in more recent years, *C. septempunctata* is no longer increasing in density at our study site (Table 4). *C. septempunctata* is a widespread invader often noted for its superior competitive ability (Hodek and Michaud 2008). In 1989, when this survey was initiated, *C. septempunctata* had already occurred in the community for 4 years (Maredia et al. 1992b), which may have represented the ‘acute’ phase in the invasion of this species. This pattern has been observed in invasions by

C. septempunctata at other locales. After its arrival in southern Manitoba, *C. septempunctata* populations increased rapidly, peaked about 5 years after introduction, and then settled into a relatively uniform pattern of variation in proportional abundance (Turnock et al. 2003). Several exotic species have a pattern of slow increase after establishment, followed by a period of rapid growth, and then a stabilization or even decline (Wheeler and Hoebeke 2008). In 2007, Harmon et al. hypothesized that *H. axyridis* would undergo a similar stabilization of its population cycling, but remarked that because of the lack of additional exotic species in the early establishment phase, it was unclear if another species would replace *H. axyridis* as the dominant coccinellid.

It is interesting to note that all exotic species were positively correlated with each other at the weekly resolution (Fig. 4a), with the exception of a lack of a relationship between *P. quatuordecimpunctata* and *C. septempunctata*. This effect could be due to the general increase in population over time of all exotic species, but then it would be expected that these relationships would also be observed at the yearly resolution (Fig. 4b). This suggests that either exotic species tend to thrive under similar conditions, or that one species may provide biotic facilitation in the invasion of another.

Dynamics in individual species

Boom-bust cycles appear to be common amongst coccinellids at our site, and these natural fluctuations highlight the importance of long-term data in understanding community dynamics. Strikingly cyclical abundances of individual species contributed to the overall variability in total coccinellid numbers from year to year (Fig. 1). Characteristic frequencies varies between species: *C. maculata*, *C. trifasciata* and *H. parenthesis* all underwent unsynchronized 2–3 year abundance cycles, which may be related to the 3 year crop rotation at the site, particularly in the case of *C. maculata*, which is known to feed on maize pollen, a species native to North America. *C. maculata* was most correlated with annual crop habitat, but *C. trifasciata* was not correlated with any habitats, and *H. parenthesis* was positively correlated with perennial crops and negatively with forest habitats (Table 4). *C. septempunctata*, however, peaked in abundance every 4–5 years, an effect that is not easily explained, *C. septempunctata* was equally correlated to annual crops

habitats, which are on a 3 year cycle, and only weakly correlated with any environmental variables (Table 4). This cycle may be related to a species-characteristic pattern in resource exploitation: a similar boom-bust cycle has been observed for *C. septempunctata* in Great Britain (H. Roy, personal communication Jan 19, 2013).

Mechanism of extirpation/displacement of native coccinellids

We did not observe declines in the majority of native coccinellid species. However, for *C. maculata* and *A. bipunctata*, our results are consistent with the competitive exploitation hypothesis, which predicts that after the arrival of a functionally similar but competitively superior exotic species, populations of native species would decline, as would prey resources (Snyder 2009). In a companion study (Bahlai et al. 2013), we found that the herbivore suppression potential of the coccinellid community at this site was largely unchanged in response to invasion. This result, coupled with increasing exotic dominance documented in this study, suggests that exotic species are more efficient at acquiring resources in agroecosystems than *A. bipunctata* and *C. maculata*. The relative degree of decline of each of these species offers some insight into the importance of each interspecies interaction. Although *A. bipunctata* is now rare at our site, *C. maculata* is still relatively common, and this is likely due to the degree of niche overlap between each species and the invaders. Although we observed no statistically significant habitat correlations for *A. bipunctata*, it has been noted elsewhere that this species is often observed with and is similar to *H. axyridis* in use of arboreal habitats and overwintering behavior (Roy et al. 2011), and thus these species likely have a high degree of niche overlap. Conversely, *C. maculata* is an omnivorous species and thus its resource needs do not overlap completely with any of the exotic species present, all of which are primarily aphidophagous (Gordon 1985; Marshall 2006). Thus, its decline, though significant, was of much lower magnitude than that of *A. bipunctata*. Indeed, in years when maize is planted at the site, its pollen presents a resource to *C. maculata* that cannot be effectively exploited by any of the exotic species. Although *C. maculata* has similar performance on the pollens of a variety of

species occurring throughout its range, its long-standing association with pollen from native maize may particularly foster this species continued presence in North American midwestern agroecosystems (Smith 1960). In recent ‘maize’ years (2008, 2011) *C. maculata* represented 45–50 % of all coccinellids captured in that given year (Table 1; Bahlai et al. 2013). Thus, the exact mechanism and magnitude of exploitation advantage will vary with each interspecies interaction, which is beyond the ability of a purely observational survey-based dataset to discern.

Numerous studies have noted competitive advantages of both *C. septempunctata* and *H. axyridis* compared to North American native species. Labrie et al. (2006) found that exotic *H. axyridis* was more voracious, completed larval development faster, and underwent supernumerary larval instars with further increased voracity, allowing it to consume many more aphids over its development than *C. maculata*. Alyokhin and Sewell (2004) found that aphid populations were substantially reduced from historical levels after *H. axyridis* arrived in Maine potato fields, suggesting that this species is more effective at depleting food resources (Alyokhin and Sewell 2004). Similarly, *C. septempunctata* produced more eggs, earlier than *C. transversoguttata* in Utah alfalfa fields (Kajita and Evans 2010), and was able to complete development under a greater variety of resource conditions than certain native species (Evans 2000). However, the relative importance of these competitive advantages will vary in determining realized competition. It can be expected that the effects of exotics on different native species partitioned between different niches will be species specific, depending on the degree of niche overlap.

Brown (2003) suggested that the interaction between *C. septempunctata* and *H. axyridis* should favor native species. Essentially, the degree of niche overlap between these two species would result in increased competitive interaction between them, negatively impacting both and freeing resources for other species. However, this effect was not observed in our system, indeed, these two species were slightly positively correlated with each other (Fig. 4a). Although the density of *C. septempunctata* was observed to be stable immediately following the arrival of *H. axyridis*, the same was true for the majority of native species. Declines were only observed in species most likely to have a fair degree of niche overlap with *H. axyridis*.

Aphid resource structure

The arrival of soybean aphid in our study system and its subsequent outbreaks in 2001, 2003 and 2005 represented the addition of a significant food source that was particularly exploited by *H. axyridis* (Bahlai and Sears 2009; Costamagna and Landis 2006; Fox et al. 2004; Heimpel et al. 2010). This perturbation to the aphid resource structure of the landscape fostered extremely high densities of *H. axyridis*, not only in annual crops, but also in nearby perennial crops (Fig. 11). Although populations of *H. axyridis* were rapidly increasing prior to 2000, and the species was already implicated in declines of certain native species (Colunga-Garcia and Gage 1998), soybean aphid outbreaks fostered a temporary biotic facilitation of the invasion of *H. axyridis*, which may now be reaching a new equilibrium (Heimpel et al. 2010; Knapp et al. 2012). During the soybean aphid's acute invasion phase in 2000–2006, the downward trend in native species diversity at the weekly resolution appears to have accelerated, and then stabilized after aphid outbreaks ceased in 2007 (Bahlai et al. 2013). This trend suggests that native coccinellids did not benefit equally from the additional food resources provided by soybean aphid, and supports the assertion that *H. axyridis* is more adept at utilizing aphids in agricultural crops (Alyokhin and Sewell 2004). Soybean aphid and *H. axyridis* have a long-standing association with soybean fields in their native range, and may, in fact, represent components of an invasional meltdown in North America (Heimpel et al. 2010).

Habitat compression

Habitat use shifts in *A. bipunctata* and *C. trifasciata* offer evidence in support of Evans's (2000, 2004) habitat compression hypothesis. In the present study, we have quantitatively shown that coccinellid communities in semi-natural and natural habitats both differ from and are more variable than coccinellid communities in cultivated habitats (Fig. 2). We also examined within-species patterns of habitat use in relation to the arrival of exotic species (Figs. 1, 3) and found that for certain native species, at least a weak habitat compression effect was observable during the period of *H. axyridis* outbreak associated with soybean aphid (Figs. 1b, e, 3a, d). *H. axyridis* is considered a habitat generalist, although it is known to dominate arboreal habitats in much of its range (Adriaens et al.

2008; LaMana and Miller 1996). Interestingly, the population density of *H. axyridis* in forest habitats dropped during the soybean aphid outbreak period compared to their densities prior to the arrival of the soybean aphid (Fig. 11), and in 2001–2002, *A. bipunctata* (Fig. 1b) and *C. trifasciata* (Fig. 1e) were observed in the forest habitats, after never being observed in these habitats in the prior 9 years. *C. trifasciata* appeared at lower-than-usual densities in annual and perennial crops during these years, and returned to these habitats by 2005, but low numbers of *A. bipunctata* continue to be observed in forest habitats, representing a statistically significant habitat use shift (Fig. 3a).

Prior to this study, evidence for (and against) the habitat compression hypothesis in coccinellid communities was indirect or based on anecdotal accounts. Evans (2000) remarked that *C. septempunctata* did not appear to dominate the coccinellid community in natural/naturalized habitats as it did in alfalfa. Later, he showed that the proportion of native coccinellids captured increased dramatically in agricultural fields artificially infested with large numbers of prey, suggesting these species were still occurring in the landscape, but less so in cultivated habitat when prey resources were depleted by exotics in crops (Evans 2004). Similarly, after the introduction of *C. septempunctata*, *C. novemnotata* and *C. transversoguttata* shifted from habitat generalists to specialized habitats in Alberta (Acorn 2007). Yet, more systemic evaluation of the hypothesis by previous authors directly examining habitat use patterns failed to gather evidence to support the habitat compression hypothesis. In one study, native coccinellids appeared in similar or even lower proportions in non-agricultural habitats after the introduction of several exotic species (Finlayson et al. 2008), and non-native species dominated coccinellid communities in meadowlands in another 2-year study (Anderies et al. 2006). Similarly, no evidence of *A. bipunctata*, *C. transversoguttata*, or *C. novemnotata* increase in refuge habitats was found in eastern South Dakota, although *A. bipunctata* occurred in wooded habitats in the western portion of the state (Hesler and Kieckhefer 2008). The habitat compression effect we observed in the present study was temporary, in the case of *C. trifasciata*, and subtle, in the case of both species, making it unlikely it would have been observed without comprehensive long term ecological monitoring using a consistent sampling protocol.

Conclusions

In our study, the decline of native coccinellids as a whole was not generalizable to a single mechanism because the responses of individual species varied dramatically over time. In fact, most native species were observed to have a net stable abundance. Decreasing overall abundance of native species was primarily driven by a decline of two previously abundant species, *A. bipunctata* and *C. maculata*, and was most likely due to competitive exploitation by exotic species. The magnitude of the decline in these two species appeared to be related to the degree of dietary overlap between the native species and the exotics. We also found evidence to support Evans' (2000) habitat compression hypothesis: several species from our site underwent an apparent habitat use shift after the establishment of *H. axyridis*. Interestingly, this effect was observed both for a species observed to be in decline (*A. bipunctata*) and, to a lesser extent, in a species observed to be stable in overall abundance (*C. trifasciata*).

Acorn (2007) argued that most observed extirpations of native coccinellids in eastern North America are caused by habitat destruction, and that the introduction of exotic coccinellids to the community results in ecological change rather than loss of ecosystem function per se. In a companion study, we found no net loss of aphid suppression nor in the overall community dynamics in this community in response to invasion (Bahlai et al. 2013), and in the current study, we found that the changes in the relative abundance of community members primarily result from a shift in the set of dominant coccinellids. Annual crop habitats are largely monocultures, and provide less variable conditions. Species which are best adapted to exploiting resources in annual monocultures will tend to dominate these habitats, and because annual monocultures are widespread, species that are favored by them will also dominate at a landscape level. In many cases, the coccinellid species able to dominate in annual systems are Eurasian exotic species co-evolved with Eurasian cropping systems, agricultural practice (i.e. annual monocultures) and pest species. This is particularly exemplified by *H. axyridis*, an efficient and voracious predator of soybean aphids, occurring on soybeans: in this case, the predator, prey and host crop are all originally from the same range in Asia (Costamagna and

Landis 2006, 2007; Heimpel et al. 2010; Ragsdale et al. 2011). However, current agricultural practice does not completely exclude native species. When a native species is able to exploit resources particular to the cropping system, such as the ability of *C. maculata* to feed on maize pollen, it enables the species to maintain its populations in agricultural landscapes.

Even if the exotic species are able to effectively replace native species within many agricultural habitats with regards to herbivore suppression function, it is still both advisable from a resilience perspective and desirable from a conservation standpoint to maintain native coccinellids, wherever possible. The occurrence of refuge habitats such as forests in agricultural landscapes support coccinellid communities which are both unique from, and more variable than, communities that occur in cultivated habitats. These unique communities may help to provide functional resilience: for example, if some disturbance prevents exotic species from depleting pest herbivores in agricultural habitats, native coccinellids are often quick to colonize these resource-rich areas (Evans 2004). It is possible that future agricultural land use expansion, particularly if dominated by annual monocultures, will decrease the number of refuge habitats, and impair the ability of North American native coccinellid species that rely on refuge habitats to persist. Thus, the intentional design of agricultural landscapes to include such refuge habitats may be important for conservation of diverse coccinellid communities.

Acknowledgments The authors would like to thank Aaron Fox, Rufus Isaacs, Helen Roy and William Snyder for helpful comments offered on an earlier draft of this manuscript, as well as the input of two anonymous reviewers. We acknowledge the numerous field assistants for weekly field data collection and data preservation. We also thank the Kellogg Biological Station Long-Term Ecological Research Management Team for their assistance with trapping logistics, and Sven Bohm for database management. Funding for this work was provided by the National Science Foundation Long Term Ecological Research program Grant #1027253 and Michigan State University AgBioResearch.

Appendix

Spearman rank correlation analysis results for abundance of 13 species of coccinellid partitioned by habitat type (Tables 2, 3, 4).

Table 2 Spearman rank correlations for species of coccinellid observed at Kellogg Biological Station, Hickory Corners, MI, 1989–2012, based on weekly observations, across all habitats, and then separately within annual crop, perennial crop and forest habitats

Species	CSEPT	CMAC	CSTIG	CTRIF	CMUND	HTRE	HAXY	HCONV	HGLAC	HPARN	HVAR	PQUA
<i>Site-wide correlations</i>												
ABIPN	0.13	0.17		0.04	0.05		-0.18	0.14	-0.04	0.05	-0.06	-0.04
CSEPT		0.07	-0.05				0.07	0.07	0.10	0.23	0.14	
CMAC			0.07	0.06	0.13	0.04	-0.08		0.04	0.13	-0.06	
CSTIG											-0.05	
CTRIF										0.05		
CMUND										0.04		0.05
HTRE							0.04					
HAXY									0.15	0.08	0.22	0.15
HCONV										0.09	0.05	
HGLAC										0.13		
HPARN											0.18	0.05
HVAR												0.18
<i>Annual crops only</i>												
ABIPN	0.12	0.08					-0.21				-0.08	
CSEPT		-0.19							0.07	0.24	0.10	
CMAC			0.07	0.07	0.30		-0.09		0.08	0.09	-0.16	0.12
CSTIG							-0.06					
CTRIF									0.11	0.08		
CMUND							0.09					0.07
HTRE							0.08					
HAXY									0.13	0.06	0.28	0.18
HCONV												
HGLAC										0.14		
HPARN											0.16	
HVAR												0.22
<i>Perennial crops only</i>												
ABIPN	0.15	0.26		0.07	0.06		-0.20	0.25			-0.05	-0.05
CSEPT		0.08	-0.05		0.10			0.09	0.10	0.18	0.09	
CMAC			0.15	0.05	0.14		-0.12	0.08		0.09	-0.06	
CSTIG												-0.06
CTRIF							-0.06					
CMUND										0.06		
HTRE								0.09				
HAXY								-0.05	0.18	0.09	0.19	0.17
HCONV										0.12		0.05
HGLAC										0.11		
HPARN											0.17	
HVAR												0.16
<i>Forest habitats only</i>												
ABIPN												
CSEPT				0.10			0.20			0.16	0.16	

Table 2 continued

Species	CSEPT	CMAC	CSTIG	CTRIF	CMUND	HTRE	HAXY	HCONV	HGLAC	HPARN	HVAR	PQUA
CMAC				0.10			0.12					
CSTIG				0.10			0.14					
CTRIF										0.15		
CMUND							0.13		0.13			
HTRE												
HAXY											0.16	
HCONV												
HGLAC												
HPARN											0.18	
HVAR												

Only Spearman ranks where $p < 0.01$ are shown. Species abbreviations are defined in Fig. 1 legend

Table 3 Spearman rank correlations for species of coccinellid observed at Kellogg Biological Station, Hickory Corners, MI, 1989–2012, based yearly total observations, across all habitats, and then separately within annual crop, perennial crop and forest habitats

Species	CSEPT	CMAC	CSTIG	CTRIF	CMUND	HTRE	HAXY	HCONV	HGLAC	HPARN	HVAR	PQUA
<i>Site-wide correlations</i>												
ABIPN							−0.54		−0.43		−0.47	
CSEPT		0.57	0.37					0.48		0.77		
CMAC					0.36			0.38		0.61		
CSTIG												
CTRIF												
CMUND										0.33		
HTRE												
HAXY									0.53		0.64	
HCONV										0.65		
HGLAC										0.41		
HPARN												
HVAR												0.48
<i>Annual crops only</i>												
ABIPN							−0.78				−0.64	
CSEPT										0.53		
CMAC												
CSTIG												
CTRIF												
CMUND												
HTRE												
HAXY											0.72	
HCONV												
HGLAC												
HPARN												
HVAR												0.60

Table 3 continued

Species	CSEPT	CMAC	CSTIG	CTRIF	CMUND	HTRE	HAXY	HCONV	HGLAC	HPARN	HVAR	PQUA
<i>Perennial crops only</i>												
ABIPN		0.62					-0.74		-0.52		-0.65	
CSEPT										0.56		
CMAC					0.70							-0.54
CSTIG											-0.52	-0.59
CTRIF											-0.43	
CMUND												
HTRE												
HAXY									0.60			
HCONV										0.54		
HGLAC												
HPARN												
HVAR												
<i>Forest habitats only</i>												
ABIPN												
CSEPT												
CMAC												
CSTIG							0.60					
CTRIF											0.70	
CMUND												
HTRE												
HAXY												
HCONV												
HGLAC												
HPARN												
HVAR												

Only Spearman ranks where $p < 0.01$ are shown. Correlations between species each accounting for greater than 1 % of captures are in bold. Species abbreviations are defined in Fig. 1 legend

Table 4 Spearman rank correlations for species of coccinellid observed at Kellogg Biological Station, Hickory Corners, MI, 1989–2012 with environmental and habitat variables at weekly and yearly temporal resolutions

Parameter	ABIPN	CSEPT	CMAC	CSTIG	CTRIF	CMUND	HTRRE	HAXY	HCONV	HGLAC	HPARN	HVAR	PQUA
<i>Weekly</i>													
Day of year		-0.04	-0.04	-0.17	-0.05	0.20		0.15	0.08		0.04	0.11	
Degree day accumulation		-0.05	-0.04	-0.19	-0.05	0.18		0.19	0.06		0.05	0.16	
Mean temperature		0.12		-0.08	0.06			0.08			0.05	0.08	0.13
Precipitation		-0.05		0.04				-0.04					
Annual crop		0.26	0.29	-0.11		-0.10	0.05		0.06		0.08	0.12	
Perennial crop		-0.07	-0.13	0.08		0.08	-0.04	0.04				-0.05	
Forest	-0.04	-0.27	-0.21					-0.05	-0.06	-0.07	-0.15	-0.09	-0.04
<i>Yearly total</i>													
Year	-0.57		-0.42					0.53				0.61	0.71
Degree day accumulation				-0.32									
Mean temperature													0.35
Precipitation													
Annual crop		0.39	0.55										
Perennial crop				0.35		0.47					0.43		
Forest		-0.69	-0.74						-0.49	-0.40	-0.75		

Only Spearman ranks where $p < 0.01$ are shown. Species abbreviations are defined in Fig. 1 legend

References

- Acorn J (2007) Invasion of the seven-spotted certainty snatchers. *Am Entomol* 53:191–192
- Adriaens T, Martin San, y Gomez GSM, Maes D (2008) Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. In: Roy HE, Wajnberg E (eds) From biological control to invasion: the ladybird *Harmonia axyridis* as a model species. Springer, Dordrecht, pp 69–88
- Alyokhin A, Sewell G (2004) Changes in a lady beetle community following the establishment of three alien species. *Biol Invasions* 6:463–471
- Anderies JM, Ryan P, Walker BH (2006) Loss of resilience, crisis, and institutional change: lessons from an intensive agricultural system in southeastern Australia. *Ecosystems* 9:865–878
- Bahlai CA, Sears MK (2009) Population dynamics of *Harmonia axyridis* and *Aphis glycines* in Niagara Peninsula soybean fields and vineyards. *J Entomol Soc Ont* 140:27–39
- Bahlai CA, Colunga-Garcia M, Gage SH et al (2013) Long term functional dynamics of an aphidophagous coccinellid community are unchanged in response to repeated invasion. *PLoS One* 8:e83407
- Brown MW (2003) Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *Biocontrol* 48:141–153
- Clarke K, Gorley R (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth
- Colunga-Garcia M, Gage SH (1998) Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. *Environ Entomol* 27:1574–1580
- Costamagna AC, Landis DA (2006) Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecol Appl* 16:1619–1628
- Costamagna AC, Landis DA (2007) Quantifying predation on soybean aphid through direct field observations. *Biol Control* 42:16–24
- Cottrell TE (2005) Predation and cannibalism of lady beetle eggs by adult lady beetles. *Biol Control* 34:159–164
- Dysart RJ (1988) The European lady beetle *Propylea quatuordecimpunctata*: new locality records for North America (Coleoptera: Coccinellidae). *J N Y Entomol Soc* 96:119–121
- Elliott N, Kieckhefer R, Kauffman W (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* 105:537–544
- Evans EW (2000) Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in western North America. *Eur J Entomol* 97:469–474
- Evans EW (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology* 85:637–647
- Evans EW, Soares A, Yasuda H (2011) Invasions by ladybugs, ladybirds, and other predatory beetles. *Biocontrol* 56:597–611
- Finlayson CJ, Landry KM, Alyokhin AV (2008) Abundance of native and non-native lady beetles (Coleoptera: Coccinellidae) in different habitats in Maine. *Ann Entomol Soc Am* 101:1078–1087
- Foley JA, Coe MT, Scheffer M et al (2003) Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in northern Africa. *Ecosystems* 6:524–532
- Fox TB, Landis DA, Cardoso FF et al (2004) Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ Entomol* 33:608–618
- Gagnon A-E, Heimpel GE, Brodeur J (2011) The ubiquity of intraguild predation among predatory arthropods. *PLoS One* 6:e28061
- Gardiner MM, O'Neal ME, Landis DA (2011) Intraguild predation and native lady beetle decline. *PLoS One* 6:e23576
- Gardiner MM, Allee LL, Brown PMJ et al (2012) Lessons from lady beetles: accuracy of monitoring data from US and UK citizen-science programs. *Front Ecol Environ*. doi:10.1890/110185
- Gordon RD (1985) The Coccinellidae (Coleoptera) of America North of Mexico. *J N Y Entomol Soc* 93:i-912
- Gordon RD (1987) The first North American records of *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae). *J N Y Entomol Soc* 95:307–309
- Harmon JP, Stephens E, Losey J (2007) The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *J Insect Conserv* 11:85–94
- Harrell Jr FE, Dupont C (2013) Package 'Hmisc' for R v. 3.12-2
- Hautier L, San Martin G, Callier P et al (2011) Alkaloids provide evidence of intraguild predation on native coccinellids by *Harmonia axyridis* in the field. *Biol Invasions* 13:1805–1814
- Heimpel G, Frelich L, Landis D et al (2010) European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. *Biol Invasions* 12:2913–2931
- Hesler LS, Kieckhefer RW (2008) Status of exotic and previously common native coccinellids (Coleoptera) in South Dakota landscapes. *J Kans Entomol Soc* 81:29–49
- Hodek I, Honek A (1996) Ecology of Coccinellidae. Kluwer Academic, Dordrecht
- Hodek I, Michaud JP (2008) Why is *Coccinella septempunctata* so successful? (A point-of-view). *Eur J Entomol* 105:1–12
- Kajita Y, Evans E (2010) Alfalfa fields promote high reproductive rate of an invasive predatory lady beetle. *Biol Invasions* 12:2293–2302
- Kajita Y, Obrycki J, Sloggett J et al (2010) Intraspecific alkaloid variation in ladybird eggs and its effects on con- and hetero-specific intraguild predators. *Oecologia* 163:313–322
- Kenis M, Auger-Rozenberg M-A, Roques A et al (2009) Ecological effects of invasive alien insects. *Biol Invasions* 11:21–45
- Knapp AK, Smith MD, Hobbie SE et al (2012) Past, present, and future roles of long-term experiments in the LTER Network. *Bioscience* 62:377–389
- Koch RL (2003) The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *J Insect Sci* 3:1–16
- Krassoi FR, Brown KR, Bishop MJ et al (2008) Condition-specific competition allows coexistence of competitively superior exotic oysters with native oysters. *J Anim Ecol* 77:5–15
- Labrie G, Lucas É, Coderre D (2006) Can developmental and behavioral characteristics of the multicolored Asian lady

- beetle *Harmonia axyridis* explain its invasive success? Biol. Invasions 8:743–754
- LaMana ML, Miller JC (1996) Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biol Control 6:232–237
- Maredia K, Gage S, Landis D et al (1992a) Ecological observations on predatory Coccinellidae (Coleoptera) in south-western Michigan. Gt Lakes Entomol 25:265–270
- Maredia KM, Gage SH, Landis DA et al (1992b) Habitat use patterns by the seven-spotted lady beetle (Coleoptera: Coccinellidae) in a diverse agricultural landscape. Biol Control 2:159–165
- Marshall SA (2006) Insects- their natural history and diversity: with a photographic guide to insects of Eastern North America. Firefly Books, Richmond Hill
- Michaud JP (2002) Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. Environ Entomol 31:827–835
- Musser FR, Nyrop JP, Shelton AM (2004) Survey of predators and sampling method comparison in sweet corn. J Econ Entomol 97:136–144
- Ostrom PH, Colunga-Garcia M, Gage SH (1996) Establishing pathways of energy flow for insect predators using stable isotope ratios: field and laboratory evidence. Oecologia 109:108–113
- Raak-van den Berg CL, De Lange HJ, Van Lenteren JC (2012) Intraguild predation behaviour of ladybirds in semi-field experiments explains invasion success of *Harmonia axyridis*. PLoS One 7:e40681
- Ragsdale DW, Landis DA, Brodeur J et al (2011) Ecology and management of the soybean aphid in North America. Annu Rev Entomol 56:375–399
- R Development Core Team (2012) R: a language and environment for statistical computing 2.15.3. R Foundation for Statistical Computing
- Reitz SR, Trumble JT (2002) Competitive displacement among insects and arachnids. Annu Rev Entomol 47:435–465
- Rhainds M, Yoo HJS, Kindlmann P et al (2010) Two-year oscillation cycle in abundance of soybean aphid in Indiana. Agric For Entomol 12:251–257
- Rosenheim JA, Kaya HK, Ehler LE et al (1995) Intraguild predation among biological-control agents: theory and evidence. Biol Control 5:303–335
- Roy H, Brown P, Frost R et al (2011) Ladybirds (Coccinellidae) of Britain and Ireland. Natural Environment Research Council (NERC), Swindon
- Smith BC (1960) A technique for rearing coccinellid beetles on dry foods, and influence of various pollens on the development of *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae). Can J Zool 38:1047–1049
- Smith CA, Gardiner MM (2013) Oviposition habitat influences egg predation of native and exotic coccinellids by generalist predators. Biol Control 67:235–245
- Snyder WE (2009) Coccinellids in diverse communities: which niche fits? Biol Control 51:323–335
- Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. Annu Rev Ecol Evol Syst 37:95–122
- Takizawa T, Snyder WE (2012) Alien vs. predator: could biotic resistance by native generalist predators slow lady beetle invasions? Biol Control 63:79–86
- Turnock WJ, Wise IL, Matheson FO (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. Can Entomol 135:391–404
- van de Koppel J, Rietkerk M, Weissing FJ (1997) Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends Ecol Evol 12:352–356
- Wheeler AG, Hoebeke ER (2008) Rise and fall of an immigrant lady beetle: is *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) still present in North America? Proc Entomol Soc Wash 110:817–823
- Woltz JM, Landis DA (2013) Coccinellid immigration to infested host patches influences suppression of *Aphis glycines* in soybean. Biol Control 64:330–337