



Landscape composition influences patterns of native and exotic lady beetle abundance

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ABSTRACT

Aim Coccinellid beetles are important predators that contribute to pest suppression in agricultural landscapes. Since the introduction of the exotic coccinellids *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas into the USA, several studies have reported a decline of native Coccinellidae in agroecosystems. We aimed to investigate the influence of landscape composition on native and exotic coccinellid abundance within soybean fields.

Location Iowa, Michigan, Minnesota and Wisconsin.

Methods As part of a 2-year study (2005–06) on the biological control of the soybean aphid, *Aphis glycines* Matsumura, we examined coccinellid communities in 33 soybean fields using yellow sticky card traps. Landscape heterogeneity and composition were measured at multiple spatial scales ranging 1–3.5 km from focal soybean fields where coccinellid sampling took place.

Results Exotic species made up 90% of the total coccinellid community in Michigan soybean fields followed by Wisconsin (84%), Minnesota (66%) and Iowa (57%). *Harmonia axyridis* was the dominant exotic coccinellid in all states comprising 45–62% of the total coccinellid community, followed by *C. septempunctata* (13–30%). Two additional exotic species, *Hippodamia variegata* (Goeze) and *Propylea quatuordecimpunctata* (L.) were also found in the region. Overall, the most abundant native coccinellid was *Hippodamia convergens* Guerin-Meneville; however, its abundance varied across the region, comprising 0% (Michigan) to 28% (Iowa) of the total coccinellid community. Landscape structure significantly influenced the composition of coccinellid communities in soybean agroecosystems. We found that native coccinellids were most abundant in low-diversity landscapes with an abundance of grassland habitat while exotic coccinellids were associated with the abundance of forested habitats.

Main conclusion We propose that grassland dominated landscapes with low structural diversity and low amounts of forested habitat may be resistant to exotic coccinellid build-up, particularly *H. axyridis* and therefore represent landscape-scale refuges for native coccinellid biodiversity.

Keywords

Coccinellidae, *Harmonia axyridis*, landscape, native species decline.

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INTRODUCTION

Across the majority of the north-central USA, agricultural ecosystems form a human-mediated landscape matrix containing small patches of formerly dominant natural habitats.

Natural habitats may serve as source populations of organisms which colonize the highly disturbed matrix, influencing the abundance of pest and beneficial insects and the ecosystem services such as biocontrol and pollination they provide in croplands (Steffan-Dewenter *et al.*, 2002; Thies *et al.*, 2003;

Tscharntke *et al.*, 2005; Marino *et al.*, 2006; Gardiner *et al.*, 2009). Landscapes supply both native and exotic species to agricultural ecosystems resulting in agricultural food webs containing introduced species at each trophic level. Although habitat loss and the introduction of exotic species are considered the major threats to native biodiversity (Wilcove *et al.*, 1998), little is known about how land-use influences the abundance of native species and their exotic competitors in agricultural landscapes. Didham *et al.* (2007) found that of 11,588 studies that examined the influence of land-use change and 3528 studies that examined the effects of invasion, only 1.2% considered both potential impacts on native biodiversity. From a conservation and ecosystem services perspective, it is critical to determine how these factors influence populations of native species. Herein, we investigate the influence of landscape composition on populations of declining native Coccinellidae and their exotic competitors.

The use of exotic lady beetles in classical biological control projects was fuelled by the success of the vedalia beetle, *Rodalia cardinalis* (Mulsant), introduced from Australia to suppress populations of the cottony cushion scale, *Icerya purchasi* Maskell, in 1889. Since this early biological control effort, over 100 species of exotic lady beetles have been either intentionally or accidentally released into North America (Harmon *et al.*, 2007). Although a majority of introduced exotics are not known to affect native communities, a small number of species have been implicated as contributing to native coccinellid decline. The two most prominent of these are *Coccinella septempunctata* L. and *Harmonia axyridis* Pallas. Intentional introductions of *C. septempunctata* began in 1958 and over the next few decades, beetles were released in several states (Schaefer *et al.*, 1987). *Harmonia axyridis* was first detected in the USA in 1988 (Chapin & Brou, 1991). Like *C. septempunctata*, this species was intentionally released; but its eventual establishment has been attributed to an accidental introduction via shipping (Day *et al.*, 1994). In the north-central USA, two additional exotic species have been detected recently; *Propylea quatuordecimpunctata* (L.) (Gardiner *et al.*, 2009) and *Hippodamia variegata* (Goeze) (Gardiner & Parsons, 2005). Both species were released as part of an effort at biological control of the Russian wheat aphid (Ellis *et al.*, 1999).

Although exotic coccinellid species contribute to biological control of agricultural pests (Cardinale *et al.*, 2003; Snyder & Evans, 2006; Costamagna & Landis, 2007; Gardiner & Landis, 2007), increasing evidence suggests that some species of exotic lady beetles may also displace native coccinellid species (Putnam, 1955; Wheeler & Hoebeke, 1995; Elliott *et al.*, 1996; Colunga-Garcia & Gage, 1998; Michaud, 2002; Alyokhin & Sewell, 2004; Snyder *et al.*, 2004; Harmon *et al.*, 2007). Since the establishment of *C. septempunctata* and *H. axyridis*, declines in the abundance of *Adalia bipunctata* (L.), *Brachiantha ursina* (F.), *Chilocorus stigma* (Say), *Coccinella novemnotata* Herbst, *Coccinella transversoguttata richardsoni* Brown, *Cycloneda munda* (Say) and *Hippodamia tredecimpunctata* (Say) have been documented in the USA (Wheeler &

Hoebeke, 1995; Elliott *et al.*, 1996; Colunga-Garcia & Gage, 1998; Alyokhin & Sewell, 2004; Losey *et al.*, 2007).

Like many natural enemies, adult coccinellids are transient predators, foraging within several habitats during the growing season (Evans, 2003). Therefore, their diversity and abundance are likely to depend on both the abundance of prey within crop habitats and the structure and composition of the surrounding landscape (Marino & Landis, 1996; Colunga-Garcia *et al.*, 1997; Elliott *et al.*, 1999; Thies *et al.*, 2003; Tscharntke *et al.*, 2005; Gardiner *et al.*, 2009). Landscape variables such as habitat composition, quality and patchiness as well as dispersal capability, all impact the abundance of coccinellids in agricultural crops (Elliott *et al.*, 1999; Thies *et al.*, 2003; Schmidt & Tscharntke, 2005).

Several recent studies show that coccinellids supply a valuable ecosystem service to soybean farmers (Landis *et al.*, 2008), suppressing populations of the soybean aphid, *Aphis glycines* Matsumura, an invasive pest of soybean in the USA (Venette & Ragsdale, 2004; Fox *et al.*, 2005; Costamagna & Landis, 2007; Gardiner & Landis, 2007; Chacón *et al.*, 2008; Gardiner *et al.*, 2009). Given the patterns of native species decline and the importance of landscape diversity and composition in supplying beneficial insects to croplands, we were interested in determining if soybean fields in landscapes that varied in diversity and composition were colonized by a similar community of coccinellids. Our objectives were to: (1) measure variation in the composition of the coccinellid community across the north-central states of Iowa, Michigan, Minnesota and Wisconsin, and (2) determine if the abundance of native and exotic coccinellids was related to the diversity and composition of the surrounding landscape. Our hypothesis was that landscapes with a high proportion of natural habitat such as forests and grasslands would supply the greatest abundance of coccinellids to soybean fields.

METHODS

Field sites

From early June through mid August in 2005 and 2006, we examined the abundance of exotic and native coccinellids in 33 soybean fields in Iowa, Michigan, Minnesota and Wisconsin (Appendix S1). Twenty-two sites were part of a USDA Risk Avoidance and Mitigation (RAMP) funded multi-state study of soybean aphid management. In each RAMP site, a randomized complete block design with four to six blocks and either 4 (2005) or 5 (2006) treatments was established in 0.4 ha (2005) or 0.2 ha (2006) plots. Multiple experiments occurred within these fields; the study reported here was conducted in control plots not treated with insecticide. Additionally, 11 sites were located in commercial production fields (two in 2005 and nine in 2006), each containing four 0.4 ha (2005) or 0.2 ha (2006) untreated plots. Each year, a minimum distance of 20 km separated each site. Across years, we maintained the relative regional distribution of soybean fields, but sampled different sites. The average distance

between soybean sites sampled in 2005 or 2006 within a given region was 2.4 km (range = 0.2–14.6 km, Appendix S1). Field size averaged 16.0 ha (range = 13.6–48.1 ha).

Aphid and coccinellid sampling

Beginning in June of 2005 and 2006 and continuing until mid to late August, coccinellid diversity and abundance was estimated by placing an unbaited yellow sticky card (PHEROCON AM; Great Lakes IPM, Vestaburg, MI, USA) in each plot at all study sites (four cards per site in both 2005 and 2006). Yellow sticky card traps have been shown to be an effective sampling technique for coccinellids in croplands, with greater capture efficiency than other sampling techniques such as visual plant counts or vacuum sampling (Mensah, 1996; Parajulee & Slosser, 2003; Schmidt *et al.*, 2008). In the centre of each plot, a metal 'T' fence post was erected with holes every 10 cm vertically. A 0.61-cm-diameter dowel was placed through a hole so a 22.9 × 27.9 cm sticky card could be suspended just above the plant canopy. As plants grew, the dowel was moved up the post to keep the trap just above canopy level. Sticky traps were replaced every 7 days. All adult coccinellids were counted and identified to species and the number per trap was averaged across all sampling dates for each site. We measured prey availability as a potential predictor of coccinellid abundance by conducting weekly destructive whole plant counts during the timeframe of the coccinellid sampling. In each plot, five randomly selected plants were removed from the ground and the number of apterous and alate aphids was counted on each plant. For analysis, prey abundance was averaged across all sampling dates for each site.

Landscape analysis

Field geospatial data were collected using a handheld GPS receiver using Wide Area Augmentation System correction. The spatial coordinate for the centre of each site was used to obtain ortho-rectified digital aerial imagery. We digitized the habitats surrounding each study site to a radius of 3.5 km using ARC GIS 9.1 (ESRI, Redlands, CA, USA). Aerial images were captured between 1998 and 2006. Land-use changes between the image date and study period were recorded by ground-verification in June–August annually, with corrections made during the digitization process. At the same time, we also determined the specific land cover ($n = 25$ categories) present in all areas of each landscape (Appendix S2). Some locations included polygons that were not visible from a roadway and permission to access private lands could not always be obtained. These polygons were given a value of zero and were excluded from further analysis. The area of each site that could not be identified varied from 0 to 4.5%. The smallest polygons identified included field plots on university research farms and small patches of fallow field ($< 5 \text{ m}^2$); the largest were contiguous urban areas, lakes and forests ($< 11.9 \text{ km}^2$).

Landscape heterogeneity was measured using Simpson's Index (D) (Simpson, 1949). Simpson's Index is typically used to examine the variance of species abundance distributions. Here we applied it to examine variance in the proportion of area covered by each of 25 land-cover categories. Simpson's Index was used to measure the influence of overall heterogeneity or 'patchiness' of a landscape on coccinellid abundance; it does not directly indicate that the presence of particular types of habitat is important in the abundance of these species. Using methods modelled after Thies *et al.* (2003), we measured landscape heterogeneity at six spatial scales ranging from 1- to 3.5-km radii (at 0.5-km intervals) from the field centre. The equation for Simpson's Index (D) is: $D = 1/\sum(p_i)^2$ where p_i is the proportion of habitat in the i th land-cover category (D increases as heterogeneity increases).

Statistical analysis

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

To evaluate the relationship between coccinellid abundance and landscape variables, we performed a principal components analysis (PCA) on the landscape variables to reduce the dimensions of the data. Seven landscape variables comprising four crop and three non-crop variables were included in the PCA analysis (Appendix S2). These represent seven broad categories of land-cover present within the 3.5-km-radius landscape circles. Land cover was combined into these seven categories to meet the assumption of a multivariate normal distribution of the variables, as many types of land cover were only present in a small number of the 33 landscapes and could not be analysed separately. The three most abundant crops present in the 3.5-km-radius landscapes circles: Corn, Soybean and Wheat were included as separate variables. The fourth variable was 'Other Crops', which included all other crops planted within a 3.5-km radius of our soybean sites. This included many regionally-important and small acreage specialty crops, which were present in a small number of the 33 landscapes. The three non-crop variables were Forest, Grassland and Urban. The Forest variable included all forested land, the majority of which was deciduous forest. Some landscapes also included small acreages of planted conifers as well as mixed stands of conifers and deciduous trees. The Grassland variable included all perennial habitats lacking dominant woody vegetation. This included old field and restored prairie, grazed pasturelands and forage crops. The final non-crop variable was Urban, which included residential and urban areas. The water and wetlands variable (Appendix S2) was dropped from the PCA as this habitat constituted a low

(< 2%) percentage of the majority of landscapes. Principal component axes were extracted using correlations among variables and the resulting factors were not rotated (McCune & Mefford, 1999). We restricted our analysis to the first two eigenvectors, which explained between 51.3 and 57.3% of the variability in landscape data. This was done for each spatial scale (1.0–3.5 km radii).

Akaike's Information Criterion, adjusted for a small sample size (AIC_c) was used as a model selection procedure to examine the influence of six variables on the abundance of native and exotic Coccinellidae (Burnham & Anderson, 2002). These variables were: Year (year site was sampled, 2005 or 2006), Prey (average abundance of soybean aphid present in each site), Exotic (average abundance of exotic Coccinellidae present in each site, used only in native Coccinellidae models), D (Simpson's Index), PC1 (principal component 1 interpreted from PCA) and PC2 (principal component 2 interpreted from PCA). The D -variable measured the influence of overall landscape heterogeneity, while the inclusion of the variables PC1 and PC2 allowed us to measure the influence of specific landscape attributes on coccinellid abundance. For exotic coccinellids, 17 models were compared: an intercept only model, sampling year model and models containing all combinations of the two interpreted principal components, D and prey abundance (Appendix S3). For native coccinellids, 33 models were compared including an intercept only model, sampling year model and models containing all combinations of the two interpreted principal components, D , prey abundance and exotic coccinellid abundance (Appendix S3). At each spatial scale, we present the model with the minimum AIC_c value, i.e. with the best support for the data and any competing models with a AIC_c difference of < 2 (Riic & Sample, 2001; Burnham & Anderson, 2002). For each model,

we present the maximum log-likelihood estimate, the Akaike weights, which estimate the relative likelihood of a given model against all other models and AIC_c differences (Δ_i). We calculated adjusted r^2 for the minimum AIC_c model and competing models to evaluate how well the models explained the variation in the data. We define the best overall model as the model with the lowest AIC_c score across all spatial scales. We calculated partial correlations for all variables in models with more than one predictor. Partial correlations were used to assess the importance of individual independent variables after adjusting for additional variables in the model. After determining the most predictive spatial scale for native and exotic coccinellids, we examined the relationship between the 17 (exotic species) or 33 (native species) models and the two most abundant species of exotic and native coccinellid. The AIC_c analysis and adjusted r^2 were determined using R version 2.1.1 (R Development Core Team 2005). Partial correlations were obtained using PROC CANCORR in SAS v. 9.1 (SAS Institute 1999). The mean number of native and exotic coccinellids, mean numbers of individual coccinellid species as well as mean prey abundance were $\log(x + 1)$ transformed prior to analysis to meet the assumptions of normality and homogeneity of variances (SAS Institute, 1999).

While no site had an overlapping 3.5-km landscape buffer within a given year, 24 sites did have overlapping buffers across years. Therefore, prior to interpreting the results of the AIC_c analysis, we examined potential spatial autocorrelation of the residuals of the best fit and competing models for all response variables. This was done between each site and the nearest neighbouring site using Moran's I -statistic. We did not find significant spatial autocorrelation between neighbouring sites for any of the best fit or candidate models examined for any response variable.

Table 1 Coccinellid community composition in soybean fields in Iowa, Michigan, Minnesota and Iowa in 2005–06.

	Percentage of total Coccinellidae				Mean Coccinellidae per sticky trap \pm SEM			
	Iowa	Michigan	Minnesota	Wisconsin	Iowa	Michigan	Minnesota	Wisconsin
Exotic species								
<i>Harmonia axyridis</i>	44.5	52.8	46.2	61.5	0.83 \pm 0.07	0.98 \pm 0.07	0.68 \pm 0.10	1.29 \pm 0.12
<i>Coccinella septempunctata</i>	12.8	30.0	19.5	22.6	0.24 \pm 0.03	0.55 \pm 0.05	0.29 \pm 0.05	0.47 \pm 0.06
<i>Hippodamia variegata</i>	0	5.6	0	0.20	0	0.10 \pm 0.02	0	0.004 \pm 0.004
<i>Propylea quatuordecimpunctata</i>	0	1.6	0	0	0	0.03 \pm 0.01	0	0
All exotic species	57.2	90.0	65.6	84.3	1.08 \pm 0.07	1.65 \pm 0.09	0.97 \pm 0.11	1.75 \pm 0.14
Native species								
<i>Hippodamia convergens</i>	28.3	0	19.5	4.9	0.53 \pm 0.06	0	0.29 \pm 0.06	0.10 \pm 0.02
<i>Coleomegilla maculata</i>	5.1	5.6	6.2	2.2	0.10 \pm 0.02	0.10 \pm 0.02	0.09 \pm 0.03	0.05 \pm 0.02
<i>Hippodamia parenthesis</i>	3.0	0.9	3.1	4.5	0.06 \pm 0.01	0.02 \pm 0.01	0.05 \pm 0.02	0.09 \pm 0.02
<i>Hippodamia tridecimpunctata</i>	0.4	0.3	1.0	3.7	0.01 \pm 0.003	0.01 \pm 0.003	0.02 \pm 0.01	0.08 \pm 0.05
<i>Cycloreda munda</i>	4.8	2.6	4.6	0.4	0.09 \pm 0.01	0.05 \pm 0.01	0.07 \pm 0.02	0.01 \pm 0.01
<i>Chilocorus stigma</i>	0	0.6	0	0	0	0.01 \pm 0.01	0	0
<i>Anatis labiculata</i>	0.5	0	0	0	0.01 \pm 0.01	0	0	0
<i>Brachiacantha ursine</i>	0.7	0.1	0	0	0.01 \pm 0.01	0.002 \pm 0.002	0	0
All native species	44.8	10.0	34.4	15.7	0.81 \pm 0.07	0.33 \pm 0.06	0.51 \pm 0.08	0.33 \pm 0.06
Total Coccinellidae					1.88 \pm 0.10	1.82 \pm 0.09	1.47 \pm 0.14	2.08 \pm 0.16

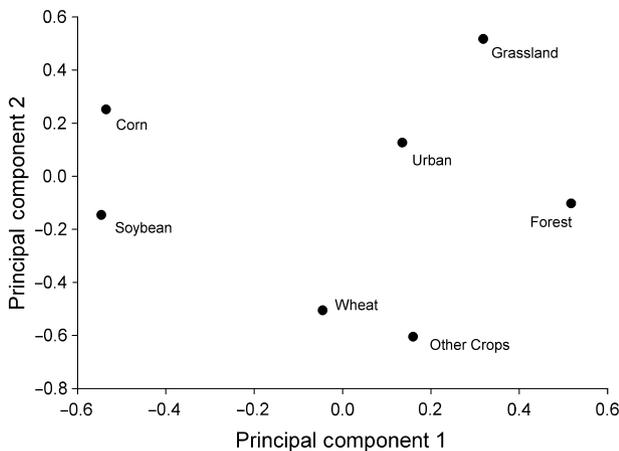


Figure 1 Principal components analysis (PCA) ordination for principal components 1 and 2 of landscape elements surrounding soybean fields sampled at a radius of 1.5 km. Points indicate the principal component loadings of each variables included in the PCA analysis. Sites with positive loadings on PC1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

RESULTS

Coccinellid diversity and abundance across the region

Four exotic and eight native species of coccinellids were observed on sticky cards in 2005 and 2006 (Table 1) across our study area in the north-central USA. There were significant differences in the composition of this community across the four states ($\chi^2_{24} = 756.34, P < 0.0001$). Michigan had the highest percentage of exotic coccinellids (90.0%) followed by Wisconsin (84.3%) (Table 1). Exotic species were less

dominant in Minnesota and Iowa, comprising 65.6 and 57.2% of the coccinellid communities respectively. In all four states, the most abundant exotic species was *H. axyridis* followed by *C. septempunctata*. Two additional exotic species were detected: *H. variegata* in Michigan and Wisconsin and *P. quatuordecimpunctata* in Michigan.

The most abundant native species was *Hippodamia convergens* Guerin-Meneville, which comprised a greater proportion of the community in Iowa (28.3%) and Minnesota (19.5%) compared with Michigan (0%) and Wisconsin (4.9%). The second most abundant native species was *Coleomegilla maculata* Timberlake, which comprised 2.2–6.2% of the coccinellids detected in soybean fields (Table 1).

Landscape heterogeneity (D)

The landscape surrounding each of our field sites varied from agriculturally dominated to forest and grassland-dominated. Within the 3.5-km landscape radius surrounding each of the 33 sites, *D*-values ranged from 2.4 to 6.4. The percentage of the landscape composed of annual cropland ranged from 11 to 91%. Landscapes with high and low percentages of annual cropland were sampled in each state (Michigan 11–91%, Wisconsin 20–71%, Minnesota 44–84% and Iowa 27–89%). At a 3.5-km radius, grassland habitat comprised 1–69% (Michigan 1–21%, Wisconsin 4–21%, Minnesota 6–18% and Iowa 5–69%), while forested habitat comprised 0–58% of the landscape surrounding field sites (Michigan 3–32%, Wisconsin 3–58%, Minnesota < 1–16% and Iowa 0–6%).

Principal component analysis of landscape variables

Both of the principal components interpreted in this study were measures of landscape composition (Fig. 1). PC1 was correlated with the variable Forest, while negative loadings on PC1 were correlated with the variables Corn and Soybean.

Table 2 Summary of model selection statistics for evaluating the abundance of exotic Coccinellidae. The first model listed at each spatial scale is the minimum AIC_c model; bold indicates the best overall model. Only models with a *A_i* of 2 or less are included as competing models.

Radius (km)	Model	Log-likelihood	<i>K_i</i>	AIC _c	<i>A_i</i>	<i>W_i</i>	Adjusted <i>r</i> ²	Partial correlations
1.0	<i>B₀ + B₁ PCI*</i>	-5.75	3	18.34	0.00	0.23	0.13	
1.0	<i>B₀ + B₁ PCI* + B₂ Prey</i>	-4.52	4	18.48	0.14	0.22	0.17	PC1 = 0.43, Prey = 0.27
1.5	<i>B₀ + B₁ PCI*</i>	-4.55	3	15.94	0.00	0.30	0.19	
1.5	<i>B₀ + B₁ PCI** + B₂ Prey</i>	-3.46	4	16.36	0.42	0.24	0.22	PC1 = 0.49, Prey = 0.25
2.0	<i>B₀ + B₁ PCI**</i>	-3.73	3	14.30	0.00	0.35	0.23	
2.0	<i>B₀ + B₁ PCI** + B₂ Prey</i>	-2.85	4	15.14	0.84	0.23	0.25	PC1 = 0.52, Prey = 0.23
2.5	<i>B₀ + B₁ PCI**</i>	-4.15	3	15.14	0.00	0.35	0.21	
2.5	<i>B₀ + B₁ PCI** + B₂ Prey</i>	-3.31	4	16.06	0.92	0.22	0.22	PC1 = 0.50, Prey = 0.22
3.0	<i>B₀ + B₁ PCI*</i>	-4.45	3	15.74	0.00	0.35	0.20	
3.0	<i>B₀ + B₁ PCI* + B₂ Prey</i>	-3.72	4	16.88	1.14	0.20	0.21	PC1 = 0.48, Prey = 0.21
3.5	<i>B₀ + B₁ PCI*</i>	-4.66	3	16.16	0.00	0.34	0.19	
3.5	<i>B₀ + B₁ PCI* + B₂ Prey</i>	-3.94	4	17.32	1.16	0.19	0.19	PC1 = 0.47, Prey = 0.21

Significant at **P* < 0.05, ***P* < 0.01.

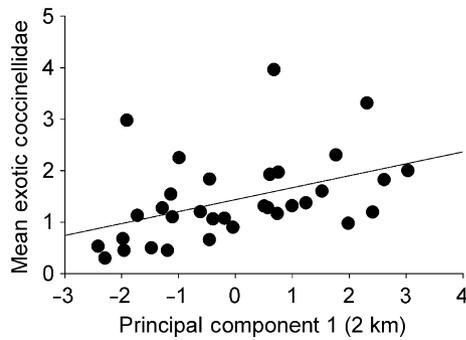


Figure 2 Relationship between the mean weekly catch of all exotic Coccinellidae from yellow sticky card traps and the overall best fit model, PC1 at 2 km. Models were compared using an AIC_c model selection procedure. Untransformed data are shown, data were $\log(x + 1)$ transformed for analysis.

Therefore, sites with positive values of PC1 suggest a landscape with an abundance of wooded habitat, while sites with negative values of PC1 indicate a landscape dominated by corn and soybean agriculture (Fig. 1). For PC2, sites with positive loadings were correlated with the variable Grassland and negative loadings were correlated with the variables Other

Crops and Wheat. Sites with high values of PC2 had a high proportion of pastures, old fields and restored prairies (Fig. 1). Sites with negative values had a high proportion of locally important fruit, vegetable, ornamental and small grain crops. Both principal components indicate the intensity of landscape disturbance, with high values indicating less disturbed grassland and forested habitats and low values indicating greater agricultural disturbance.

Model fitting of relationships between native and exotic coccinellid abundance, prey and landscape variables

For exotic coccinellids, the PC1 model had the lowest AIC_c value and the PC1 + Prey model was a competing model at all spatial scales examined (radii of 1–3.5 km) (Table 2). The PC1 model at 2 km was the best fit model overall, with the lowest AIC_c value across spatial scales. PC1 was a significant predictor of exotic coccinellid abundance ($P = 0.003$, 2 km). Exotic coccinellid abundance was the highest in soybean fields in landscapes with an abundance of forested habitat (Fig. 2). In the competing PC1 + Prey model, prey abundance was not a significant predictor of exotic coccinellid abundance ($P = 0.209$, 2 km).

Table 3 Summary of model selection statistics for evaluating the abundance of native Coccinellidae. The first model listed at each spatial scale is the minimum AIC_c model; bold indicates the best overall model. Only models with a Δ_i of 2 or less are included as competing models.

Radius (km)	Model	Log-likelihood	K_i	AIC_c	Δ_i	W_i	Adjusted r^2	Partial correlations
1.0	$B_0 + B_1$ (Year)*	2.90	3	1.04	0.00	0.34	0.18	
1.5	$B_0 + B_1$ (Year)*	2.90	3	1.04	0.00	0.21	0.18	
1.5	$B_0 + B_1$ (D)*	2.58	3	1.68	0.64	0.15	0.16	
1.5	$B_0 + B_1$ (D)* + B_2 PC2	3.47	4	2.50	1.46	0.10	0.18	$D = -0.42$, PC2 = 0.34
2.0	$B_0 + B_1$ (D)* + B_2 PC2*	5.11	4	-0.78	0.00	0.21	0.26	$D = -0.36$, PC2 = 0.37
2.0	$B_0 + B_1$ (D) + B_2 PC2* + B_3 (Exotic)	5.61	5	0.98	1.76	0.09	0.25	$D = -0.32$, PC2 = 0.38, Exotic = -0.17
2.0	$B_0 + B_1$ (Year)*	2.90	3	1.04	1.82	0.09	0.18	
2.0	$B_0 + B_1$ PC2*	2.81	3	1.22	2.00	0.08	0.17	
2.5	$B_0 + B_1$ (D)* + B_2 PC2*	4.92	4	-0.40	0.00	0.20	0.25	$D = -0.35$, PC2 = 0.37
2.5	$B_0 + B_1$ (Year)*	2.90	3	1.04	1.44	0.10	0.18	
2.5	$B_0 + B_1$ PC2*	2.76	3	1.32	1.72	0.09	0.17	
2.5	$B_0 + B_1$ (D) + B_2 PC2* + B_3 (Exotic)	5.37	5	1.46	1.86	0.08	0.24	$D = -0.32$, PC2 = 0.38, Exotic = -0.16
3.0	$B_0 + B_1$ (D) + B_2 PC2*	4.77	4	-0.10	0.00	0.17	0.24	$D = -0.30$, PC2 = 0.40
3.0	$B_0 + B_1$ PC2*	3.21	3	0.42	0.52	0.13	0.19	
3.0	$B_0 + B_1$ (Year)*	2.90	3	1.04	1.14	0.10	0.18	
3.0	$B_0 + B_1$ PC2* + B_2 (Exotic)	3.92	4	1.60	1.70	0.07	0.20	PC2 = 0.46, Exotic = -0.20
3.0	$B_0 + B_1$ (D) + B_2 PC2* + B_3 (Exotic)	5.24	5	1.72	1.82	0.07	0.24	$D = -0.28$, PC2 = 0.40, Exotic = -0.17
3.0	$B_0 + B_1$ (PCL) + B_2 PC2*	3.85	4	1.74	1.84	0.07	0.20	PC1 = -0.19, PC2 = 0.47
3.5	$B_0 + B_1$ (D) + B_2 PC2*	5.09	4	-0.74	0.00	0.17	0.25	$D = -0.28$, PC2 = 0.44
3.5	$B_0 + B_1$ PC2**	3.77	3	-0.70	0.04	0.17	0.22	
3.5	$B_0 + B_1$ (PCL) + B_2 PC2**	4.45	4	0.54	1.28	0.09	0.23	PC1 = -0.20, PC2 = 0.50
3.5	$B_0 + B_1$ PC2** + B_2 (Exotic)	4.34	4	0.76	1.50	0.08	0.22	PC2 = 0.49, Exotic = -0.18
3.5	$B_0 + B_1$ (Year)*	2.90	3	1.04	1.78	0.07	0.18	
3.5	$B_0 + B_1$ (D) + B_2 PC2* + B_3 (Exotic)	5.53	5	1.14	1.88	0.07	0.25	$D = -0.26$, PC2 = 0.43, Exotic = -0.16

D = Simpson's Index where $D = 1/\sum(p_i)^2$ and p_i , proportion of habitat in the i th land-cover category.

Variables in parentheses indicate a negative relationship with native Coccinellidae abundance.

Significant at * $P < 0.05$, ** $P < 0.01$.

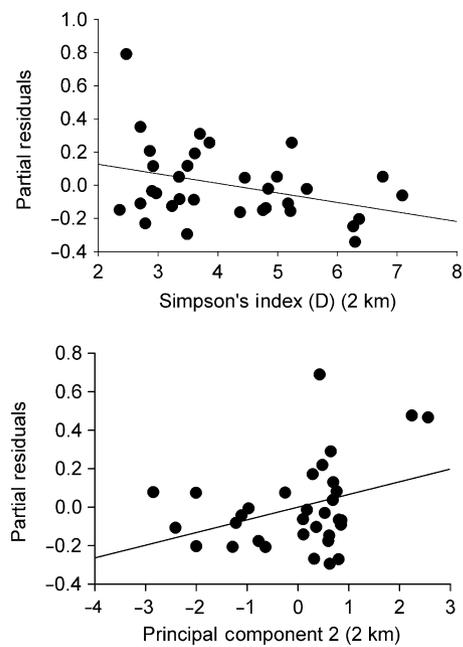


Figure 3 Partial residual plots illustrate the relationship between the mean weekly catch of all native Coccinellidae from yellow sticky card traps and the best fit model $D + PC2$ at 2 km determined using an AIC_c model selection procedure.

For native coccinellids, the best fit and candidate models varied by spatial scale (Table 3). The Year model had the lowest AIC_c value at spatial scales of 1–1.5 km, whereas at radii of 2–3.5 km, the $D + PC2$ model had the lowest AIC_c value. Several competing models were found across spatial scales including Year, PC2, D , $D + PC2$, PC1 + PC2, PC2 + Exotic and $D + PC2 + Exotic$. The $D + PC2$ model at 2 km had the lowest AIC_c value across spatial scales (Table 3). Native species were significantly correlated with both predictors in this model, being most abundant in low diversity landscapes (D , $P = 0.043$ at 2 km) with an abundance of grassland (PC2, $P = 0.038$ at 2 km) (Fig. 3).

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

A radius of 2 km was the most predictive landscape scale for both exotic and native Coccinellidae; therefore, the relationship between individual species and the 17 (exotic) or 33 (native) models were compared at this spatial scale. For both exotic and native coccinellids, the best fit and competing models varied by species. The best fit model for *H. axyridis* was PC1 + Prey, with no competing models (Appendix S4). The abundance of *H. axyridis* increased with PC1 ($P = 0.002$) and prey abundance ($P = 0.022$) (Fig. 4a,b). This species was more abundant in soybean fields with a high abundance of soybean aphid within forested landscapes versus soybean fields with low prey abundance in landscapes dominated by soybean and corn fields. For *C. septempunctata*, the intercept model had the lowest AIC_c value. Competing models included PC1, Prey and

D (Appendix S4). For *H. convergens*, the Exotic + PC2 + D was the best fit model; competing models included PC2 + D , Exotic + PC2 and PC1 + PC2 (Appendix S4). This species was most abundant in soybean fields with low exotic coccinellid populations (Exotic, $P = 0.086$) within low diversity landscapes (D , $P = 0.056$) with an abundance of grassland habitat (PC2, $P = 0.002$) (Fig. 4c–e). For *C. maculata*, the PC1 model had the lowest AIC_c value; the intercept model was a competing model. There was a marginally significant negative correlation between the abundance of *C. maculata* and PC1 ($P = 0.087$), indicating that this species was less abundant in soybean fields within forested landscapes compared with corn and soybean dominated landscapes (Fig. 5).

DISCUSSION

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

Native and exotic coccinellid populations in soybean fields

Our study illustrates that temporal, within-field and landscape variables all influence the abundance of coccinellids in soybean fields. Year was a significant predictor of native coccinellids with populations higher in 2005 than 2006. We did not see a significant correlation between the within-field average soybean aphid abundance and trap catches of native Coccinellidae; however, yearly differences may be tied to variation in the abundance of *A. glycines* across the study region. On average, soybean aphid was more abundant in 2005 compared with 2006 across the four states studied. Fields with particularly high aphid populations may have acted as sources of native species, resulting in greater foraging across the landscape. An alternative

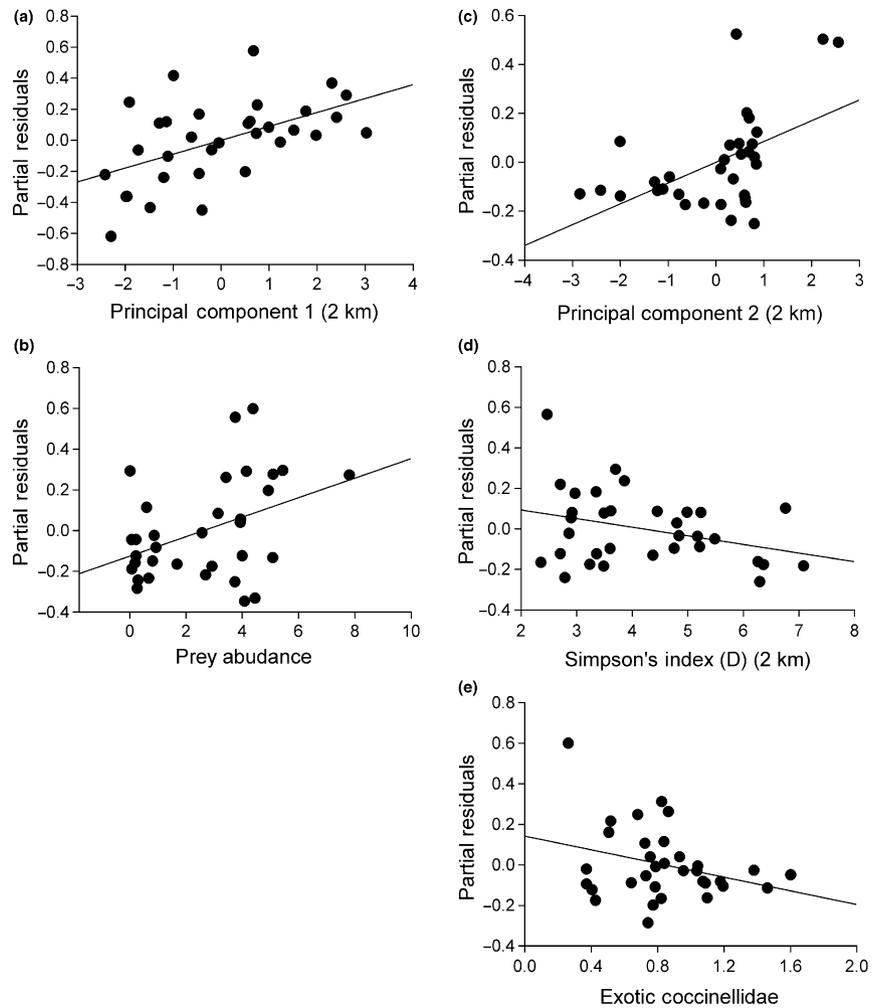


Figure 4 Partial residual plots illustrating the relationship between the mean weekly catch of the exotic lady beetle *Harmonia axyridis* (a,b) from yellow sticky card traps and components of the best fit model PC1 + Prey and *Hippodamia convergens* (c–e) and its best fit model PC2 + *D* + Exotic at 2 km determined using an AIC_c model selection procedure.

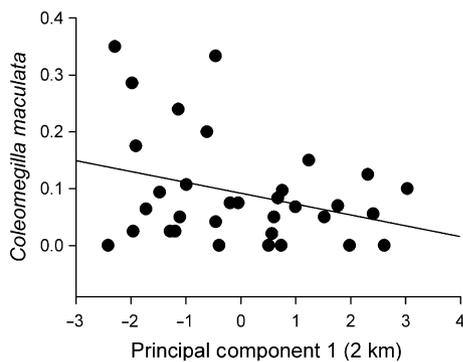


Figure 5 Relationship between the mean weekly catch of *Coleomegilla maculata* from yellow sticky card traps and the overall best fit model, PC1 at 2 km. Models were compared using an AIC_c model selection procedure. Untransformed data are shown, data were $\log(x + 1)$ transformed for analysis.

explanation for the significant year effect is the positive correlation between the abundance of *H. axyridis* and soybean aphid. This coccinellid is an important biological control agent of *A. glycines* (Gardiner & Landis, 2007) and may act as more of an *A. glycines* specialist than the other coccinellids sampled.

Increases in populations of this species with soybean aphid may have led to greater intraguild predation pressure on native species in late 2005, reducing overwintering and 2006 populations.

Landscape variables were also significant predictors of native and exotic coccinellid abundance. Landscapes with an abundance of forested habitat supported larger populations of *H. axyridis* in soybean fields. The forested habitats present in these landscapes are highly fragmented within an agricultural matrix. This type of landscape has an abundance of habitat edge and variation in vertical structure, which may favour a species such as *H. axyridis*, which is arboreal in its native range (Chapin & Brou, 1991). This coccinellid is highly mobile and disperses in and out of forest patches throughout the growing season (Gardiner, 2008). It also exhibits a hypsotactic behaviour when searching for overwintering sites, flying to prominent objects in the landscape (Koch 2003) such as forest edges. We propose that a landscape lacking abundant forested habitat may limit the success of *H. axyridis* and potentially its impacts on native coccinellids. None of the landscape variables measured was an important predictor of *C. septempunctata* abundance. This may be because *C. septempunctata* is a habitat generalist (Obryckii *et al.*, 1999) and less influenced by

landscape structure. Alternatively, *C. septempunctata* may favour perennial habitats such as grasslands and forage crops (Evans, 2004) over annual croplands such as soybean, leading to only an incidental presence in soybean.

The native coccinellid, *H. convergens*, increased in soybean fields within low diversity landscapes with an abundance of perennial grassland habitat. These included pasturelands, perennial forage crops, restored prairies and old fields. We hypothesize that perennial landscape elements provide early season prey and overwintering habitat for native species, while not supporting high populations of exotic competitors. These perennial habitats may serve as source populations of native species such as *H. convergens* that disperse into annual cropping systems such as soybean embedded within the landscape. While the negative correlation between *H. convergens* and landscape heterogeneity (*D*) is seemingly counter-intuitive, landscapes with the high heterogeneity contained higher proportions of forested habitat, while grassland patches were frequently embedded in low diversity agricultural landscapes. A negative correlation between *C. maculata*, the second most abundant native species, and PC1 indicates that this species was also more abundant in agricultural landscapes lacking significant forested habitat.

Coccinellidae and landscape scale

We measured the response of coccinellid species to landscape structure at six spatial scales ranging from a 1- to 3.5-km radius from the focal soybean field. Season-long coccinellid populations were best predicted by the abundance of forests for exotic species and grasslands for native species at a radius of 2.0 km. These results are consistent with other studies examining the abundance of herbivores, natural enemies and biocontrol services (Thies *et al.*, 2003; Schmidt & Tscharnke, 2005). Gardiner *et al.* (2009) found that the amount of biocontrol services supplied by a landscape to soybean fields was correlated with increased landscape diversity at a radius of 1.5 km surrounding soybean fields. Thies *et al.* (2003) found that herbivory and parasitism in wheat fields were positively correlated with percentage non-crop area at landscape diameter of 1.5 km.

Implications

Our study demonstrates that native and exotic coccinellids are favoured by different types of landscapes. It is possible that native species like *H. convergens* and *C. maculata* may be adapted to open savanna and prairie landscapes that formerly dominated large areas of the north-central USA and may still favour landscapes with an abundance of open grassland and field crop habitat. However, this does not explain the decline in native coccinellids in the last few decades, long after landscapes were transformed by human settlement. Alternatively, native species may only thrive in landscapes less favourable to exotic species such as *H. axyridis*, which is known to be a strong intraguild predator. If *H. axyridis* is

favoured by forested habitat, lack of forests in portions of Minnesota and Iowa may restrict the abundance and dominance of this species. *Harmonia axyridis* was detected in 1994 in both Michigan and Iowa (Colunga-Garcia & Gage, 1998; Rice, 2006) and therefore it does not appear that these differences are simply the result of time since establishment. Instead, we propose that landscape structure may be limiting the success of *H. axyridis* in intensely agricultural landscapes and allowing persistence of native coccinellid communities in such regions. If so, understanding the role of perennial grasslands in supporting source populations of native coccinellids is a conservation priority. Evans (2000) discussed the habitat compression hypothesis where, after the introduction of an exotic, native species decline in agricultural habitats and are forced back into ancestral habitats where prey are sufficient to maintain populations. We must determine if the different types of perennial grassland, such as pasturelands, restored prairies and abandoned old fields vary in their ability to support native species. Within these habitats, an understanding of the amount competitive displacement or intraguild predation pressure from exotics incurred by native populations will demonstrate which serve as important refuges.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location of 33 soybean fields sampled for coccinellids in 2005 (fields 1–13) and 2006 (fields 14–33) in Iowa, Michigan, Minnesota and Wisconsin. Sites were selected so that the 3.5-km landscape radius surrounding each field varied in diversity and the abundance of natural and agricultural habitat.

Appendix S2 Simpson's Diversity (D) and principal components analysis (PCA) categories.

Appendix S3 Models compared for exotic (17 models) and native (33 models) Coccinellidae by AIC_c analysis at spatial scales of 1.0–3.5 km.

Appendix S4 Summary of model selection statistics for *Harmonia axyridis*, *Coccinella septempunctata*, *Hippodamia convergens* and *Coleomegilla maculata* at a spatial scale of 2 km (radius). The first model listed for each species is the minimum AIC_c model (bold). Only models with a Δ_i of 2 or less are included as competing models.

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