Coccinellid response to landscape composition and configuration

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Abstract

1 Arthropod natural enemies provide valuable pest suppression in agricultural landscapes. Natural enemy abundance and diversity within a given crop, in turn, have frequently been shown to be positively related to the amount of semi-natural habitat in the landscape. However, other aspects of landscape structure may also influence natural enemy communities and may be more amenable to management.

2 We simultaneously assessed the relationship among several metrics of landscape structure, as well as between these metrics and coccinellid activity in soybean fields. We used partial least squares regression to examine the coccinellid response to landscape structure.

3 Coccinellid activity was lowest in landscapes dominated by annual crops grown in large fields and highest in landscapes dominated by semi-natural habitats such as grasslands and forests, with a higher diversity of crops grown in smaller fields.

4 Landscape characteristics, including composition factors such as the type and amount of different land covers and configuration factors such as the interspersion of these land covers, are often correlated within a set of landscapes. Isolating the effects of individual landscape characteristics on natural enemy communities will be necessary to move forward with the development of management actions that can increase biocontrol services in agroecosystems.

Keywords Agricultural landscape, biological control, Coccinellidae, landscape composition, landscape configuration.

Introduction

Agricultural landscapes benefit from ecosystem services such as pollination and natural pest control (Power, 2010). In the U.S.A., native and naturalized natural enemies provide pest suppression services to agricultural landscapes worth an estimated $4.6 billion annually (Losey & Vaughan, 2006). The ultimate success of pest suppression is dependent upon the provision of natural enemies to crop fields by the surrounding landscape. Landscape structure affects the composition of insect communities and the abundance of individual species, which in turn can lead to higher biocontrol rates and less crop damage in more complex landscapes (Thies & Tscharntke, 1999).

In studies of landscape effects on natural enemies, it is common practice to use the amount of semi-natural habitat in the landscape as a metric of landscape complexity (Burel *et al.*, 2013). Semi-natural habitats can provide natural enemies with food resources and shelter during disturbances in crop fields

(Bianchi *et al.*, 2006), leading to higher natural enemy abundance (Colunga-Garcia *et al.*, 1997; Gardiner *et al.*, 2009a), species richness (Schmidt *et al.*, 2005) and fecundity (Bommarco, 1998). Consequently, the amount of semi-natural habitat in the landscape has been related to higher herbivore suppression and reduced herbivory (Thies *et al.*, 2003).

Although the amount of semi-natural habitat has been shown to be positively related to natural enemy abundance and diversity, it may also be highly correlated with other landscape characteristics, such as overall habitat or land cover diversity (Thies & Tscharntke, 1999; Steffan-Dewenter *et al.*, 2002; Roschewitz *et al.*, 2005). These other landscape characteristics may also influence natural enemy communities. Multiple land covers in a local area may provide the different resources needed by a single organism (Dunning *et al.*, 1992). For example, a predatory insect may require one type of land cover for overwintering and another type for foraging and egg-laying. As such, land cover diversity within the landscape has also been positively related to natural enemy abundance (Isaia *et al.*, 2006) and to herbivore suppression (Kruess, 2003; Gardiner *et al.*, 2009a).

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Although much emphasis has been placed on the benefits of semi-natural habitats and overall habitat diversity, landscape characteristics related to cropping systems themselves could also benefit insect communities. For example, perennial crops may provide many of the same benefits as semi-natural habitat, such as providing prey and host resources and experiencing fewer disturbances than more intensively managed annual crops (Landis *et al.*, 2000). Landscapes that contain more perennial crops have been found to have higher spider activity density (Öberg *et al.*, 2007) and greater diversity of aphid predators (Elliott *et al.*, 1999). Similarly, landscapes with more perennial crops were found to have lower pest aphid establishment and survival (Östman *et al.*, 2001). Furthermore, just as perennial crops may provide benefits similar to those of semi-natural habitats, crop diversity may provide benefits similar to those of overall habitat diversity. In particular, crops with different phenologies may provide complementary resources at different times of the year (Vasseur *et al.*, 2013).

Similar to crop-related features, the influence of landscape configuration on natural enemies has also been largely overlooked (Burel *et al.*, 2013). Yet the spatial arrangement of habitats within a landscape can affect the rate of arrival of natural enemies into crop fields (Bianchi *et al.*, 2006), which in turn can influence natural enemy efficacy (Hogg & Daane, 2010). In particular, modelling has shown that an even distribution of semi-natural habitats within a landscape should facilitate the colonization of fields by natural enemies (Bianchi & van der Werf, 2003), suggesting that landscapes with small crop fields and a greater distribution of semi-natural habitat could promote higher natural enemy abundances in crop fields.

Ladybird beetles (Coleoptera: Coccinellidae) are generalist predators in a variety of agricultural landscapes (Colunga-Garcia *et al.*, 1997; Obrycki & Kring, 1998). In the north central U.S.A., coccinellids are of primary importance for the suppression of soybean aphid *Aphis glycines* (Costamagna & Landis, 2007; Costamagna *et al.*, 2007). Although coccinellids in this region come out of overwintering in March or April (LaMana & Miller, 1996), soybean is not planted until May or June. Therefore, the population of coccinellids in soybean in the summer, and thus their ability to suppress soybean aphid, is likely dependent upon the availability of aphid resources in the surrounding landscape earlier in the year.

Previous studies of coccinellids in the north central U.S.A. have found that coccinellids are more abundant in landscapes with more semi-natural habitat (Gardiner *et al.*, 2009a; Woltz *et al.*, 2012). Semi-natural habitat may serve as over-wintering habitat for coccinellids, particularly because crop fields in this region are typically left as bare soil or crop stubble after harvest, leaving little shelter. However, as noted by Elliott *et al.* (2002b), the persistence of the landscape effects on coccinellid populations into the summer suggests that the effects are not limited to the provision of overwintering habitat. Semi-natural habitats likely also provide food resources, and the availability of prey in semi-natural habitats supports the densities of coccinellids in crops (Bianchi & van der Werf, 2004).

Additionally, coccinellid populations can be affected by the availability of aphid prey in crops (Bianchi *et al.*, 2007). Thus, the activity density of coccinellids in summer field crops may depend on the presence of prey in crops in the landscape at other times of the year. In particular, forage crops such as alfalfa are actively growing in the spring when coccinellids emerge from overwintering, and they may provide the aphid resources necessary to build coccinellid populations before soybean is planted. Because of the potential for both crop and semi-natural elements to provide aphid prey, diverse habitats within a landscape may provide more continuous access to prey resources, especially as resources within one habitat change over time.

Furthermore, empirical and theoretical data suggest that coccinellids should also respond to landscape configuration. Bianchi and van der Werf (2003) showed that an even distribution of crop and semi-natural habitat within the landscape facilitated the dispersal of lady beetles to crop patches. Additionally, in landscapes with smaller fields, more crop area will be adjacent to edges shared with other cover types (Bianchi *et al.*, 2006), which could provide easier access to food and refuge resources. Indeed, the abundance of the coccinellid *Hippodomia convergens* was found to be negatively related to patch size within the landscape (Elliott *et al.*, 2002a)

Given the potential for multiple aspects of the landscape to influence coccinellids, the present study aimed to examine the relationships among these various landscape characteristics, as well as between these landscape characteristics and coccinellid captures. Data were collected as part of a broader project examining landscape effects on soybean aphid predators, and thus were focused on coccinellid captures in soybean during the summer growing season.

Materials and methods

Sites

The present study was replicated in 17 sites across a gradient of agricultural intensification in southern Michigan, U.S.A., during the summer of 2009 (for field coordinates, see table A.2 in Woltz *et al.*, 2012). Sites ranged from 6 to 46 km apart, with a mean nearest neighbour distance of 23 km. The agriculture in this region consists of a mix of annual field crops (maize, soybean and wheat) and perennial forage crops (pasture and perennial mixes for hay). Deciduous forests and grasslands or old fields make up the primary semi-natural land cover in the area.

Coccinellid counts

Aerially dispersing coccinellids were collected in soybean fields using 22.9×27.9 cm unbaited yellow sticky traps (Pherocon AM, Great Lakes IPM, Vestaburg, Michigan). Traps were suspended from step-in plastic fence posts (Woodstream Corporate, Lititz, Pennsylvania) at plant canopy height and were replaced every week for 8 weeks in each field, from 8 June to 9 August. All coccinellids captured were identified to species in the field. The number of coccinellids captured per trap per week were used to calculate mean number of coccinellid captures per field. To help separate coccinellids supplied to soybean fields from the surrounding landscape from coccinellid reproduction within soybean fields, we randomly sampled 20 soybean

plants in each field each week for coccinellid larvae and soybean aphids.

Landscape data

For the purposes of this experiment, a 'landscape' was designated as the area encompassing a 2-km radius around each focal soybean field. We used a 2-km radius because previous studies (Gardiner *et al.*, 2009b; Woltz *et al.*, 2012) have found landscape factors at this radius to have the most explanatory power for coccinellid populations. Additionally, this range represents the possible foraging area of large species of adult lady beetles. Flights of 2 km or greater are considered migratory (i.e. entering or leaving overwintering habitat) for *Hippodamia convergens* (Hodek *et al.*, 1993), a lady beetle species of similar size and diet preferences as the dominant predators of soybean aphid. Distances of less than 2 km can be considered within the realm of short-distance foraging flight activity, which is the type of dispersal relevant for biocontrol in crop fields. Ortho-rectified digital aerial photos for each field were obtained from the Michigan Geographic Data Library (http://www.mcgi.state.mi.us/mgdl/) based on GPS coordinates collected from the centre of each field using a handheld GPS receiver. Using these photographs, habitats within a 2.0-km radius around each field were digitized as polygons using ARC GIS, version 9.3 (ESRI, Redlands, California). For linear patches (e.g. fencerows, roadside vegetation), patches 20 m wide or greater were digitized as distinct habitats. Land cover types and habitat boundaries within field sites were ground-verified, and changes from the aerial photos were noted and corrected during digitization. The specific land cover within all habitat polygons in each landscape was determined by manually assigning land cover categories to each polygon. The digitized polygon land cover layers for each site were converted to raster format in ARC GIS. The exported rasters were input into FRAGSTATS, version 4.1 (McGarigal *et al.*, 2012) to calculate landscape metrics (hereafter given in italics).

Measures of landscape composition

Abundance of primary land-covers. The total area of the three most common crop (*Maize*, *Soybean*, *Wheat*) and semi-natural (*Grasslands*, *Forests*, *Residential areas*) land covers was calculated for each landscape. *Grasslands* included old fields, prairie plantings and Conservation Reserve Program lands (areas planted to 'long-term, resource-conserving covers' to provide a variety of ecosystem services; USDA Farm Service Agency, 2013). *Residential areas* included private residences and public mowed areas such as cemeteries and municipal parks. Small woodlots were included in the *Forest* total. Additionally, the abundance of pasture, alfalfa, orchard grass and other forage crops was calculated and combined into a single variable, *Forage crops*, representing perennial agricultural crops. Other crops, including dry beans, small grains, sugar beets, clover, vegetables and fruit trees, were present in small quantities (between 0.1% and 8.1% of landscape cover). Because of their low abundance, these crops were not included in the analysis as separate land covers. They were, however, included in diversity metrics.

Cover diversity. Simpson's diversity index (SDI) (Simpson, 1949) was used as a metric of landscape heterogeneity (McGarigal *et al.*, 2012). This index is less sensitive than other diversity measures to the number of land cover types because SDI is based on the proportion of area that each habitat type constitutes rather than the absolute area, and rare habitats will contribute smaller proportions (Magurran, 2004). Therefore, it effectively describes the variance in relative abundances of habitat types without being skewed by the presence of rare habitats (Magurran, 2004). Overall habitat diversity within the landscape, $SDI_{habitat}$, was calculated using the proportional cover of every land cover type identified in ground-truthing using the formula:

$$SDI = 1 - \sum p_i^2$$

where p_i is the proportion of landscape occupied by patches of habitat type *i*. This formulation of the index varies from 0 to 1 and can be intuitively interpreted as the probability that any two randomly chosen pixels are of different composition.

In addition to overall habitat diversity ($SDI_{habitat}$), crop diversity (SDI_{crop}) was also calculated using the proportion of every crop type identified. These two metrics were not highly correlated with one another ($r^2 = 0.01$) and could represent two different pools of resources for natural enemies.

Measures of landscape configuration

Crop field size. Increasing crop field size is a characteristic of agricultural intensification at a landscape scale (Tscharntke *et al.*, 2005). Mean crop field size in each landscape was calculated using only crop land covers according to the formula for effective mesh size (MESH):

$$MESH = \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} a_{ij}^2}{A \times 10\ 000}$$

where a_{ij} is the area of patch *ij* (m²), for all patches *i* of type *j*, and *A* is the total landscape area (m²) (McGarigal *et al.*, 2012). MESH is a metric of mean size (ha) of crop field patches. Thus, landscapes with larger crop MESH values have fewer, larger crop fields and landscapes with smaller MESH values have more, smaller crop fields.

Landscape shape index. A landscape shape index was calculated to indicate the degree of intermixing of crop and semi-natural habitats in each landscape. Landscape maps were re-coded identifying each patch as either crop or semi-natural and calculated a landscape shape index (LSI):

$$LSI = 0.25E^* / \sqrt{A}$$

where 0.25 is an adjustment for raster data, E^* is the total length of the edge in the landscape (m), including the boarders of all patches identified during digitization. *A* is the total area of the landscape (m²) (McGarigal *et al.*, 2012). LSI is greater than or equal to 1, with 1 indicating a landscape comprised of a single

large patch. LSI increases as the amount of edge in the landscape increases. LSI is a measure of both the total amount of edge existing between land covers of different types and of habitat aggregation. As a particular land cover becomes more dispersed throughout a landscape, the amount of edge increases. Thus, higher LSI values represent landscapes with greater dispersion of crop and semi-natural habitat, whereas lower LSI values represent landscapes in which crop and semi-natural habitats are aggregated into larger patches.

Statistical analysis

We used a partial least squares (PLS) regression approach (PROC PLS in SAS, version 9.2; SAS Institute Inc., Cary, North Carolina) to model variation between the landscape variables and mean coccinellid activity density. Because different species of coccinellids may respond to characteristics of the landscape differently, we also repeated the process using the mean activity density of the five most common coccinellids separately. Additionally, because we wanted to measure the influence of landscape on the provision of coccinellids to soybean fields separately from coccinellid reproduction within fields, we only used coccinellid activity data from an individual field up to the time that coccinellid larvae were observed.

The goal of PLS is to extract underlying factors, consisting of linear combinations of predictor variables that account for variation in predictor and response variables. PLS analyses can handle multiple, highly correlated predictor variables (Wold *et al.*, 2001), making it more flexible than the more commonly used multiple linear regression, in which correlated predictor variables lead to unstable parameter estimates. Using PLS regression would allow researchers to visualize the relationship between multiple correlated landscape variables and insects simultaneously, instead of using one as a proxy for all others.

It is common practice to transform predictor and response variables to achieve symmetry before conducting PLS regression (Wold *et al.*, 2001). We used a Shapiro–Wilk statistic to determine whether variables were symmetrical. We square-root transformed proportions of *Wheat*, *Forage crops*, *Residential areas*, *Grasslands* and MESH, and also cubed $SDI_{habitat}$. We then repeated Shapiro–Wilk tests to confirm that symmetry (normality) had been achieved. Results using the transformed and untransformed datasets were almost identical, and we report the results from the transformed data set to conform with standards in the published literature (Wold *et al.*, 2001).

We used one-at-a-time cross-validation to determine the appropriate number of factors to extract from the data. The number of factors that minimize the predicted residual sum of squares (PRESS) is considered the best.

After the appropriate number of factors was selected, we assessed the model's goodness of fit by examining R^2_X, R^2_Y, and Q^2. R^2_X and R^2_Y are the amount of variation in the matrix of predictor and response variables, respectively, that the extracted factors explain. Q^2 is the amount of variation in the response variable that the model predicts, as estimated through the cross-validation procedure. Briefly, a subset of data points is removed and the model is refit with the remaining data. The refit model is then used to predict the deleted response variables based on their associated predictor variables. This is repeated with different subsets of the data. The difference between the actual and predicted values for the removed data points (PRESS) from each round of cross-validation is used to calculate a Q^2 that describes the models ability to predict new observations.

We plotted the loadings of predictor and response variables for each factor to look for curvature or outliers, and examined the coefficients and variable influence on projection (VIP) values for each variable to determine the contribution of each variable to the model (Wold *et al.*, 2001). Variables with low VIP values and regression coefficients near zero have little influence on the response variable and make little contribution to the structure of the overall PLS model; thus, it is common to remove these variables and rerun the PLS to obtain a better model (SAS Institute Inc., 2011).

Results

Coccinellid captures

In 8 weeks of sampling, a total of 1903 coccinellids were captured. Mean captures per week ranged from 1.9 to 6.6 coccinellids per trap (Table 1). The coccinellid community within soybean fields was dominated by exotic coccinellids, with *Coccinella septempunctata* L. comprising 33.0%, *Harmonia axyridis* Pallas comprising 30.6%, *Propylea quatourdecimpunctata* L. comprising 19.7% and *Hippodamia variegata* (Goeze) comprising 5.9%, of all coccinellids captured. The most common native coccinellids captured were *Coleomegilla maculata* (DeGeer) and *Hippodamia parenthesis* (Say), comprising 4.6% and 2.6% of total captures. Other species comprise 1.0% or less of captures.

No coccinellid larvae were found in 11 of the 17 sites during the 8 weeks of the study (Table 1). Additionally, in four sites, larvae were only found during the eighth week of sampling. In the two remaining sites, coccinellid larvae were found at 2 and 6 weeks, respectively. Aphid density was also low in all sites (Table 1). Weekly aphid densities and coccinellid captures were not correlated for any species except *H. axyridis*. Aphid density was added to a PLS regression modelling including only *H. axyridis* as a response variable, although it was not retained as variable because it worsened the model fit.

Landscape variables

Landscapes represented a gradient from agriculturally-dominated to forest-dominated. The seven primary land covers *Maize*, *Soybean*, *Wheat*, *Forage Crops*, *Grasslands*, *Forests* and *Residential Areas* combined accounted for between 79.6% and 99.4% of all land cover in every landscape used in the study (see Supporting information, Table S1). In addition to the three most common annual crops and forage crops, several other crops were identified in the studied landscapes in lower abundances, which also contribute to crop diversity, SDI_{crop}. These included: dry beans (comprising a maximum of 8.1% of all landscapes studied), nonwheat small grains (e.g. barley, oats; 2.2%), sugar beets (1.9%), clover cover crop (1.5%), vegetables (0.3%) and

Table 1 Insect data for each focal soybean field

Site	Mean coccinellid	Mean *Coccinella septempunctata*	Mean *Harmonia axyridis*	Mean *Propylea quatourdecimpunctata*	Mean *Hippodamia variegata*	Mean *Coleomegilla maculata*	Week larvae first observed	Aphids/plant
1	2.63	1.00	0.438	0.219	0.656	0.156	NA	2.51
2	2.71	0.958	0.792	0.125	0.333	0.042	6	3.25
3	1.88	0.719	0.625	0.094	0.063	0.188	NA	0.91
4	2.34	0.625	0.750	0.406	0.063	0.094	8	2.66
5	6.34	1.563	1.781	2.375	0.063	0.438	NA	4.95
6	2.50	1.375	0.333	0.042	0.250	0.250	8	5.88
7	4.78	3.063	1.031	0.250	0.188	0.031	8	10.76
8	6.63	3.250	1.250	1.500	0.125	0.000	2	2.73
9	2.96	0.708	0.833	0.833	0.167	0.167	NA	0.43
10	4.69	1.031	0.688	1.969	0.438	0.344	NA	0.58
11	4.13	1.438	0.938	0.875	0.563	0.188	NA	0.60
12	2.06	0.719	0.469	0.656	0.000	0.156	NA	1.63
13	3.97	1.719	0.938	0.844	0.188	0.063	NA	4.48
14	2.78	0.719	1.250	0.563	0.094	0.063	8	6.55
15	2.28	0.969	0.375	0.406	0.156	0.156	NA	0.24
16	2.94	1.156	1.375	0.031	0.000	0.188	NA	2.44
17	4.22	2.344	0.844	0.500	0.219	0.188	NA	1.58

Counts for all coccinellids and the five individual species were averaged over 8 weeks, except for sites 2 and 8 in which coccinellid larvae were observed before week 8. Counts for these two sites were averaged for the weeks up to and including the first observations of coccinellid larvae.
NA, not applicable. No larvae observed.

Table 2 Model output for predictor (landscape) and response (overall coccinellid captures) variables used in partial least squares analysis

	VIP	R^2_1	R^2_2	Cumulative
Annual crops				
Soybean	0.80	62.4	0.9	63.3
Maize	0.80	61.9	8.6	70.5
Wheat	0.70	39.5	6.2	45.7
Noncrop				
Forest	1.00	55.9	39.1	95.0
Residential	1.70	79.7	14.3	94.0
Grasslands	1.10	64.4	23.5	87.9
Cover diversity				
SDI_{crop}	0.90	80.8	6.4	87.2
Configuration				
Mean field size	0.90	81.2	6.2	87.4
Landscape Shape index	0.60	32.8	4.0	36.8
Model fit				
R^2_X	–	62.1	12.1	74.2
R^2_Y	–	45.4	16.0	61.4

Variable influence for Projection (VIP) values indicate the importance of each variable for structuring the model. The percentage of variation in each predictor variable explained by Factor 1, 2, and the cumulative variation explained are given in the R^2_1, R^2_2 and cumulative columns. R^2_X and R^2_Y give the cumulative amount of variation explained for all predictor and response variables.
SDI, Simpson's diversity index.

fruit trees (0.1%). Additionally, although alfalfa, orchard grass and pastures were grouped as forage crops, they were included separately in crop diversity calculations, each contributing a maximum of 8.1%, 6.1% and 6.0% of landscapes, respectively.

PLS regression model

Initial results indicated that the *Forage* and $SDI_{habitat}$ were not important in structuring either model (e.g. low VIP values and regression coefficients near zero). Therefore, these variables were removed from further analysis.

For mean coccinellids, the model with two factors had the lowest PRESS. Factor 1 explained 62.1% of variation in the landscape predictor variables (R^2_X) and 45.4% of variation in mean coccinellid activity (R^2_Y; Table 2). Factor 2 explained an additional 12.1% of variation in landscape variables and 16.0% of variation in coccinellid activity. The two-factor model explained moderate amounts of variation in the proportion of wheat and LSI, and 63.3–95.0% of variation in the other landscape variables. The model with two factors predicted 30.7% of the variation in mean coccinellid activity (Q^2).

Factor 1 primarily explains a gradient from landscapes dominated by a few annual crops grown in large individual fields to landscapes with higher crop diversity, smaller fields and more abundant semi-natural habitats. Mean coccinellid activity, SDI_{crop}, and the abundance of *Grasslands*, *Forests* and *Residential areas* load positively with Factor 1, whereas MESH (mean field size), LSI and the abundance of *Maize*, *Soybean* and *Wheat* load negatively (Fig. 1). Factor 2 appears to differentiate types of semi-natural habitats. *Forests* loaded most negatively along Factor 2, whereas *Grasslands* loaded most positively. Factor 2 explained 39.1% of variation in forests and 23.5% of variation in grasslands.

When the five most common coccinellid species were included separately in the PLS, the model with one factor had the lowest PRESS. Factor 1 explained 62.4% of variation in the landscape predictor variables (Table 3). The predictor variables performed similarly to the previous model, with *Maize*, *Soybean*, *Wheat*,
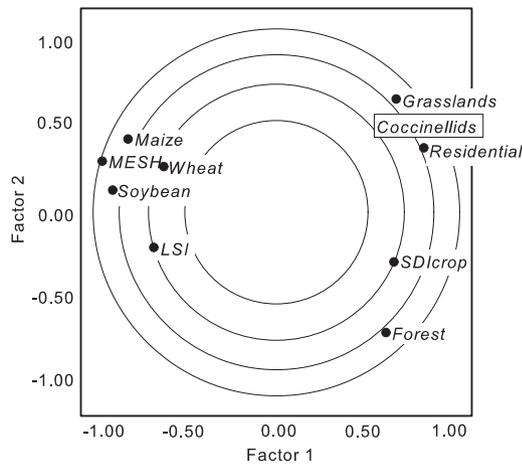
Figure 1 Loadings of response variables (overall coccinellid captures, in box) and predictor variables (landscape characteristics, bulleted) from partial least squares regression. The distance along each axis represents the amount of variation in a given variable explained by that factor. LSI, landscape shape index; MESH, mean field size; SDI, Simpson's diversity index.

LSI and MESH (mean field size) loading negatively along Factor 1. *Grasslands*, *Residential areas*, *Forests* and SDI$_{crop}$ loaded positively (Fig. 2).

The amount of variation explained in response variables varied by species. The activity of *H. axyridis* and *P. quatourdecimpunctata* were explained best at 31.4% and 39.9%, respectively. A much more modest amount was explained for *C. maculata* and *C. septempunctata* (12.7% and 9.9%). These four species load positively along Factor 1. By contrast, no variation was explained in the activity of *H. variegata*.

Discussion

We have shown that several landscape factors are both correlated with one another and related to coccinellid captures in soybean fields. In our PLS models, Factor 1 showed a gradient from landscapes dominated by the annual crops maize, soybean and wheat grown in large fields to landscapes with more grasslands, forests and residential areas, and with more types of crops grown in smaller fields. Both mean coccinellid captures and captures of four coccinellid species were higher in the landscapes with more semi-natural habitat types, higher crop diversity and smaller crop fields. Correlations among landscape variables are common (Fahrig *et al.*, 2011).

Although this level of complexity and intercorrelation is not surprising in ecology, it does make it difficult to make actionable management recommendations for increasing natural enemies in crops. Although we recognize that landscapes with a certain set of related characteristics tend to support more natural enemies, it remains unclear which specific characteristics within this set should be manipulated to foster natural enemies in agricultural landscapes. To clarify this issue, Fahrig *et al.* (2011) detail methods for careful selection of study landscapes that vary independently in key landscape variables. Although such methods may be easier in theory than practice (Fahrig *et al.*, 2011), they can help us move beyond describing patterns

Table 3 Model output for predictor (landscape) and response (five specific coccinellid species) variables used in PLS analysis

	VIP	$R^2{}_1$	$R^2{}_2$	Cumulative
Annual crops				
Soybean	0.65	61.5	0.2	61.7
Maize	0.80	64.2	8.9	73.1
Wheat	1.30	42.3	0.6	42.9
Noncrop				
Forest	0.90	59.4	31.5	90.9
Residential	1.50	77.3	11.4	88.7
Grasslands	1.15	61.2	30.1	91.3
Cover diversity				
SDI$_{crop}$	0.90	82.4	9.9	92.3
Configuration				
Mean field size	0.80	82.6	8.4	91.0
Landscape Shape index	0.55	31.0	18.1	49.1
Model fit				
$R^2{}_X$	–	62.4	13.2	75.7
R^2 *Harmonia axyridis*	–	31.4	0.9	32.3
R^2 *Propylea quatourdecimpunctata*	–	39.9	2.4	42.3
R^2 *Coccinella septempunctata*	–	9.9	7.3	17.2
R^2 *Hippodamia variegata*	–	0.0	13.4	13.4
R^2 *Coleomegilla maculata*	–	12.7	4.0	16.7
$R^2{}_Y$ cumulative	–	18.8	5.6	24.4

Variable influence for Projection (VIP) values indicate the importance of each variable for structuring the factor. The percentage of variation in each predictor variable explained by Factors 1 and 2 and the cumulative variation explained are given by $R^2{}_1$, $R^2{}_2$ and cumulative. $R^2{}_X$ and $R^2{}_Y$ give the cumulative amount of variation explained for all predictor and response variables. The amount of variation each factor explains in each species is given separately.

in landscape-natural enemy relationships to teasing out specific causal relationships that we can manage.

Furthermore, not all possible changes may be plausible. Farmers may be more willing and able to make some changes than others. The positive effects of semi-natural habitat on natural enemy abundances in crop fields have been reiterated (Thies & Tscharntke, 1999; Prasifka *et al.*, 2004; Schmidt & Tscharntke, 2005; Gardiner *et al.*, 2009a; Woltz *et al.*, 2012). However, it remains unlikely that farmers will remove substantial amounts of land from production to increase semi-natural area. Therefore, shifting our focus to benefits that can be generated from different types of crop practices may help move us toward more feasible management recommendations. For example, in the present study, both crop diversity and coccinellid activity were positively associated with Factor 1. Crop diversity is ultimately decided by the number of crops farmers choose to incorporate into their rotations. The number of crops in a rotation will be limited by the knowledge necessary to grow each crop and the specialized equipment needed for production of particular crops, as well as climate. However, careful selection of even a few crops with complementary phenologies can help provide food and shelter resources to natural enemies continuously through the growing season (Vasseur *et al.*, 2013). For example, pairing spring cereal crops with summer field crops can help natural enemy populations persist (Vasseur, 2012).

In the present study, we focused on the provision of coccinellids to a specific crop during the brief summer growing
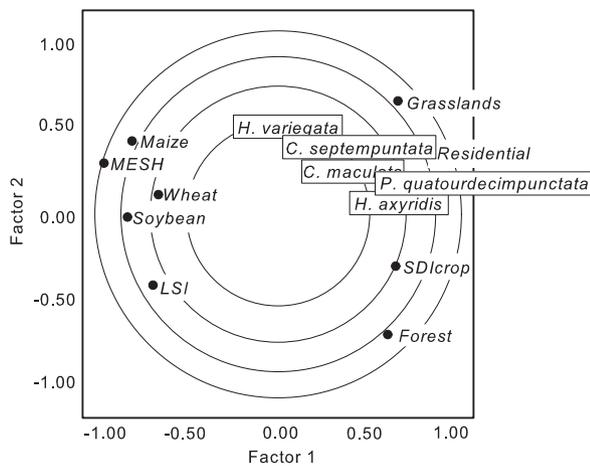
Figure 2 Loadings of response variables (specific coccinellid species, in boxes) and predictor variables (landscape characteristics, bulleted) from partial least squares regression. Although one factor minimized the predicted residual sum of squares for this model, the second factor is pictured here for clarity. The distance along each axis represents the amount of variation in a given variable explained by that factor. LSI, landscape shape index; MESH, mean field size.

season. Our results would likely have changed if we collected coccinellids in multiple habitats or for a longer portion of the year. Coccinellid communities are known to vary throughout the year and within different habitat types (Magagula & Samways, 2001; Snyder, 2009; Werling *et al.*, 2011). However, we did see differences in responses of the five coccinellid species that we examined to landscape characteristics. Although four species responded positively to the same landscape gradient, the degree to which this gradient explained variation in the coccinellids differed by species. Furthermore, *H. variegata* was not explained at all by this gradient. Different responses to the landscape are common for lady beetle species (Elliott *et al.*, 2002a, 2002b). Native lady beetles (other than the common species *C. maculata*) are frequently associated with herbaceous perennial habitats such as grasslands and forage crops (Gardiner *et al.*, 2009b; Werling *et al.*, 2011), whereas exotic species are associated more with forested landscapes (Gardiner *et al.*, 2009b). This may help explain the lack of an effect of perennial forage crops in our model because these native species made up only 6.2% of our total captures and were not considered individually. Furthermore, perennial forage crops were grown in both agriculturally dominated and semi-natural dominated landscapes, and so this variable did not separate along Factor 1.

Some exotic species, such as *C. septempunctata*, are often found not to respond to landscape characteristics at all, presumably because they are broad habitat generalists (Elliott *et al.*, 2002a; Gardiner *et al.*, 2009b). Therefore it is unsurprising that our landscape model described so little variation in this species. Other species show inconsistent responses to the landscape. *Coleomegilla maculata* has been positively related to landscape-scale forest cover in some studies (Elliott *et al.*, 2002a) and negatively related to forest cover in others (Gardiner *et al.*, 2009b). This species is pollenivorous (Hodek & Honek, 1996) and therefore likely responds to a different set of resource drivers than other species collected in the present study.

The general relationship between mean lady beetle activity and the landscape gradient described by Factor 1 appears to be driven by the response of *H. axyridis* and *P. quatourdecimpunctata*. *Harmonia axyridis* is known to be associated with forests (Gardiner *et al.*, 2009b) and is considered at least semi-arboreal, feeding on homopterans on trees (Chapin & Brou, 1991; LaMana & Miller, 1996). This species is also common nuisance species in residential areas. The tendency of *H. axyridis* to seek out prominent vertical structures can result in overwintering aggregations on houses and other buildings (Koch, 2003). Additionally, these two species were the two most common lady beetles collected as part of a citizen science project examining lady beetle communities in residential areas, suggesting that they regularly use residential habitats (Gardiner *et al.*, 2012).

The relationships between coccinellids and our configuration metrics have less obvious support in the literature. The size of an individual field could influence coccinellid immigration into that field. Smaller fields have greater perimeter to area ratios than larger ones, making it more likely that migrating coccinellids would encounter a soybean edge (Grez *et al.*, 2004). Alternatively, the negative relationship between field size and coccinellids could be an artefact of landscape change and crop cover. In this region, the landscapes in which the most maize and soybean are grown tend to have fertile soils and flat, well-drained land, allowing these crops to be grown in larger fields. Similarly, the inverse relationship between LSI and coccinellids may be the result of correlations between LSI and other variables that are stronger drivers of coccinellid activity density. For example, coccinellids are highly correlated with the amount of semi-natural habitats. In the landscapes in this dataset that had the most semi-natural habitat, that habitat was aggregated into large forest patches, which would generate lower LSI values. Therefore, the strong effect of semi-natural habitat on coccinellids could be driving this counter-intuitive relationship. The inability to determine whether these results are a result of correlations between predictor variables or actual influences on coccinellids emphasizes the need for both careful landscape selection and careful interpretation of data.

There is growing evidence that crop pest populations cannot be effectively managed without consideration of landscape influences (Cumming & Spiesman, 2006; Schellhorn *et al.*, 2008). In a previous study, we showed that providing flowering resources increased coccinellid density at field edges but not within soybean fields. Instead, the density of coccinellids within soybean fields was related to the semi-natural habitat in the surrounding landscape, regardless of the presence or absence of flowering resources at field edges, suggesting that landscape-scale action may be necessary to manage biocontrol services (Woltz *et al.*, 2012). Isolating the effects of specific characteristics of landscape structure will be necessary to move forward with respect to determining management actions that can increase natural enemy populations in agroecosystems. Furthermore, redirecting our efforts to focus more on aspects of crop production that could benefit natural enemies could help open a dialogue with the farmers managing agricultural landscapes, and lead to the development of management recommendations that they are more likely to adopt.

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Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12064

Table S1. Landscape variables calculated for a circle of 2-km radius around each focal soybean field in which coccinellids were collected. Land cover data are the proportion of each landscape consisting of that land cover.

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