



## Landscape composition influences the activity density of Carabidae and Arachnida in soybean fields

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### ABSTRACT

The distribution and abundance of semi-natural and crop habitats within agricultural landscapes is likely to greatly influence population dynamics of ground-dwelling arthropods. We investigated the influence of landscape heterogeneity and composition on the pitfall trap catch of Carabidae, Araneae, and Opiliones in soybean fields. Although we hypothesized that each predator group would increase with landscape heterogeneity and the amount of semi-natural habitat; we found variation in the response of the study organisms. The activity density of Araneae supported our hypothesis, increasing in soybean fields in landscapes with an abundance of forests and grasslands. The diversity of Carabidae in soybean fields increased in landscapes with an abundance of grassland habitat but the activity density of Carabidae declined. This decline was driven extensively by the species *Poecilus chalcites* which was less abundant in fields located within grassland-rich landscapes. Opiliones declined with increasing landscape heterogeneity but increased within forested landscapes. The spatial scale at which taxa responded to landscape composition also varied. Our hypothesis was that dispersal capacity would influence the spatial scale at which ground-dwelling arthropods responded to landscape structure. We found that Carabidae, which generally disperse by walking, responded to smaller spatial scales than linyphiid spiders, which frequently balloon. However, Lycosidae and Opiliones which also disperse mainly by walking as adults responded at larger spatial scales. These data suggest that understanding taxon-specific relationships to landscape variables should be considered in analyses of arthropod response to landscape structure.

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### 1. Introduction

Agricultural landscapes contain a diverse community of ground-dwelling arthropod natural enemies, dominated by species of Carabidae, Araneae, and Opiliones. Many of these natural enemies are habitat generalists. Whereas habitat specialists exist in patches that effectively function as islands, habitat generalists utilize a mosaic of crop and semi-natural habitats (Schmidt et al., 2005a). Wissinger (1997) suggested that natural enemies that occur in agricultural fields may colonize crops under favorable conditions and retreat to semi-natural habitats when conditions become hostile. Given this potential for dispersal among habitats, the diversity and abundance of these natural enemies available for biological control in croplands is likely to depend on the large-scale structure of the landscape matrix.

Several patterns have emerged from the study of landscape influences on natural enemy abundance, illustrating the importance of landscape composition on populations of natural enemies (Marino and Landis, 1996; Colunga-Garcia et al., 1997; Bommarco, 1998; Elliott et al., 1999; den Belder et al., 2002; Ostman, 2002; Thies et al., 2003; Weibull et al., 2003; Tschardtke and Brandl, 2004; Schmidt et al., 2005b; Tschardtke et al., 2005; Gardiner et al., 2009a,b). First, in many cases the diversity, abundance, reproductive success, and biocontrol services provided by natural enemies increase as landscape diversity and the proportion of non-crop habitat increases (Colunga-Garcia et al., 1997; Bommarco, 1998; Elliott et al., 1999) while pest number and damage decline (den Belder et al., 2002; Ostman, 2002; Thies et al., 2003; Gardiner et al., 2009a,b). Second, thresholds in landscape structure may exist below which the search efficiency and the ability of natural enemies to aggregate and control pests is diminished (Wiens et al., 1997; Thies and Tschardtke, 1999; With et al., 1999; With and King, 1999). Finally, landscape complexity may not influence all species equally, or at the same scale (Steffan-Dewenter et al., 2002; Thies et al., 2003; Schmidt and Tschardtke, 2005). Therefore,

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the arrangement and size of suitable habitat patches within a landscape are likely to have species-specific impacts on the activity of habitat generalists in agricultural croplands.

Our objective was to examine how the density of ground-dwelling predators within an annual cropland is influenced by the composition of the surrounding landscape. We examined three groups of arthropods: Carabidae, Araneae, and Opiliones in Midwestern US soybean fields. Due to the intense disturbance regime present in annual cropping systems, our hypotheses were that: (1) the density of Carabidae, Araneae, and Opiliones in soybean increases with the proportion of semi-natural habitats in the landscape (2) the overwintering phenology of a Carabidae species would affect its response to landscape composition, with species which overwinter as adults having stronger correlations with semi-natural habitat as these habitats would provide refugia (3) the spatial scale at which an organism responds to landscape structure is a function of its capacity for dispersal. Therefore those that disperse mainly by walking would respond at smaller spatial scales compared with groups known to frequently utilize flight or ballooning. We relate the patterns found herein to studies conducted in Europe and in other North American cropping systems.

## 2. Methods

### 2.1. Field sites

Between June and August of 2005 and 2006, we sampled Carabidae, Opiliones, and Araneae in 26 soybean fields in Iowa, Michigan, Minnesota, and Wisconsin (Appendix 1). Sites were selected as part of a USDA Risk Avoidance and Mitigation (RAMP) funded multi-state study of soybean aphid management (Ragsdale et al., 2007; Gardiner et al., 2009a,b). Each year, a minimum distance of 30 km separated each field site. Across years, we maintained the relative regional distribution of our sites, but sampled different soybean fields. The average distance between soybean fields sampled in 2005 and 2006 within a given region was 2.4 km (range = 0.2–14.6 km). Field size averaged 16.0 ha (range = 13.6–48.1 ha). In each RAMP field (22 sites), a randomized complete block design with 4–6 blocks and either 4 (2005) or 5 (2006) treatments was established in 0.4 ha (2005) or 0.2 ha (2006) plots within each site. Multiple experiments occurred within these fields; with this study conducted in control plots not treated with insecticide. An additional four commercial production fields (two in 2005 and two in 2006) were also included in this study, each containing four 0.4 ha (2005) or 0.2 ha (2006) untreated plots.

### 2.2. Pitfall trap sampling

Carabidae, Araneae, and Opiliones were collected from each plot using pitfall traps. One pitfall trap, consisting of a 1000 ml plastic cup with a 11.5 cm diameter opening, was placed within a soybean row in the center of each plot. All pitfall traps were a minimum of 30 m from a field edge. Cups were buried at ground level and filled with approximately 500 ml of a 50% propylene glycol solution. Each trap was covered with a rain shield constructed from a 0.9 m<sup>2</sup> section of corrugated plastic sheeting and four 0.46 m wire legs. Traps were checked weekly and all Carabidae, Araneae, and Opiliones were collected and identified. All Carabidae and Lycosidae were identified to species (Lindroth, 1968; Kaston, 1948). The remaining Araneae were identified to family (Ubick et al., 2005). Opiliones were identified to order. Differences in pitfall trap catches reflect differences in the local density and/or activity of captured animals (Southwood and Henderson, 2000). We therefore interpret the trap catches as estimating the ‘activity density’ of captured species, as has become standard in similar studies (e.g.

Lee et al., 2001; Hajek et al., 2007). For Carabidae, we also calculated species diversity using the Simpson's Index (D) (Simpson, 1949). The equation for Simpson's Index (D) is:  $D = 1/\sum(p_i)^2$  where the proportion of species  $i$  relative to the total number of species ( $p_i$ ) is determined. The reciprocal is taken for ease of interpretation (D increases as diversity increases).

### 2.3. Landscape analysis

Field geospatial data was collected using a handheld GPS receiver using Wide Area Augmentation System (WAAS) correction. The spatial coordinate for the center of each site was used to obtain ortho-rectified digital aerial imagery. We digitized the habitats surrounding each study site to a radius of 3.5 km using ARC GIS 9.1. Aerial images were captured between 1998 and 2006. Land use changes between the image date and study period were recorded by ground-verification in June–August annually, with corrections made during the digitization process. At the same time we also determined the specific land-cover ( $n = 20$  categories) present in all areas of each landscape (Appendix 2). 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 2%. The smallest polygons identified included field plots on university research farms and small patches of fallow field (<5 m<sup>2</sup>); the largest were contiguous urban areas, lakes, and forests (<11.9 km<sup>2</sup>).

Landscape diversity was measured using Simpson's Index (D) (Simpson, 1949). Simpson's Index is typically used to examine the variance of species abundance distributions. Here we applied it to examine variance in the proportion of area covered by each of 20 land use categories (Appendix 2). This index was calculated for each of the landscapes at each of the spatial scales examined. The equation for Simpson's Index (D) is:  $D = 1/\sum(p_i)^2$  where  $p_i$  = proportion of habitat in the  $i^{\text{th}}$  land-cover category (D increases as diversity increases). Using methods modeled after Thies et al. (2003) we measured landscape diversity at six spatial scales ranging from 1 to 3.5 km radii (at 0.5 km intervals) from the field center.

### 2.4. Statistical analysis

To evaluate the relationship between activity density and landscape variables, we performed a principal components analysis (PCA) on the landscape variables in order to reduce the dimensions of the data. The 20 observed land-cover categories used to calculate Simpson's diversity index were combined into eight variables included in the PCA: four crop variables (proportion corn, soybean, wheat and other crops), and four non-crop variables (proportion forest, grassland, wetland and water, and urban) (Appendix 2). Principal component axes were extracted using correlations among variables and the resulting factors were not rotated (McCune and Mefford, 1999). We restricted our analysis to the first two eigen-vectors which explained between 53.2–57.1% of the variability in landscape data. This was done for each spatial scale (1.0–3.5 km radii).

Akaike's Information Criterion, adjusted for a small sample size (AIC<sub>c</sub>) was used as a model selection procedure to examine the influence of landscape variables on Carabidae, Araneae, and Opiliones activity density (Burnham and Anderson, 2002). Seven response variables were examined, all calculated as seasonal averages by site: Carabidae (activity density of all Carabidae), adult overwintering (activity density of all adult overwintering Carabidae), larval overwintering (activity density of all larval overwintering species), Carabidae diversity (D), Araneae (activity density of all

Araneae), Lycosidae (activity density of all Lycosidae), Linyphiidae (activity density of all Linyphiidae) and Opiliones (activity density of all Opiliones). Models containing the following variables were compared for each response variable at each spatial scale (radii of 1–3.5 km): D (Simpson's Index), PC1 (principal component one interpreted from PCA), and PC2 (principal component two interpreted from PCA). For each analysis, 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<sub>c</sub> differences ( $\Delta_i$ ). We present the best-fit model, defined as the model with the minimum AIC<sub>c</sub> value, i.e. with the best support for the data, and any competing models at the spatial scale of the best-fit model that had an AIC<sub>c</sub> difference of less than two (Ribic and Sample, 2001; Burnham and Anderson, 2002). We calculated

**Table 1**

Carabidae collected from Iowa, Michigan, Minnesota, and Wisconsin soybean fields. Table indicates percentage of total catch within each state, total number collected (*N*), trophic status, and overwintering stage.

Species	Percentage of total Carabidae				<i>N</i>	Feeding <sup>a</sup>	Overwintering <sup>b</sup>
	Iowa	Michigan	Minnesota	Wisconsin			
<i>Agonum cupreum</i>	0	0.03	0	0.04	3	P	A
<i>Agonum cupripenne</i>	0.01	0.25	0	0.07	21	P	A
<i>Agonum octopunctatum</i>	0	0.03	0	0	2	P	A
<i>Agonum placidum</i>	0.07	1.49	1.55	1.56	224	P	A
<i>Amara aenea</i>	0	1.23	0.05	0.07	93	H	A
<i>Amara impunctata</i>	0	0.01	0	0	1	H	A
<i>Amara obesa</i>	0.02	0	0	0	3	H	A
<i>Amara</i> spp.	0.01	0	0	0	1	X	X
<i>Anisodactylus harrisii</i>	0.03	0	0	0	4	P	A
<i>Anisodactylus rusticus</i>	0.02	0.08	0.08	0.11	15	P	A
<i>Anisodactylus sanctaecrucis</i>	0.03	0.76	0.05	0.46	74	P	A
<i>Bembidion femoratum</i>	0	0.04	0.05	0.64	23	P	A
<i>Bembidion nitidum</i>	0	0.33	0	0.11	27	P	A
<i>Bembidion obtusum</i>	0	0.01	0	0.00	1	P	A
<i>Bembidion quadrimaculatum</i>	0	0.19	0.48	1.84	85	P	A
<i>Bembidion rapidum</i>	0.16	0.15	0	0	36	P	A
<i>Bembidion ruficolle</i>	0	0.06	0	0	4	P	A
<i>Brachinus ovipennis</i>	0	0.35	0.93	0	62	P	A
<i>Calathus gregarius</i>	0.03	0.01	0	0	5	O	A
<i>Calosoma calidum</i>	0	0	0	0.04	1	P	A
<i>Chlaenius sericeus</i>	0	0	0.05	0	2	P	A
<i>Chlaenius platyderus</i>	0.01	0	0	0	1	P	A
<i>Chlaenius pusillus</i>	0.51	0.10	0.03	0	86	P	A
<i>Chlaenius tomentosus</i>	0.01	0.00	0	0	1	P	A
<i>Chlaenius tricolor</i>	0.77	0.36	0	0.32	152	P	A
<i>Clivina bipustulata</i>	0.29	0.21	0	0	59	P	L
<i>Clivina impressifrons</i>	0.03	0.36	0	0	31	P	A
<i>Clivina</i> spp.	0.01	0	0	0.04	2	X	X
<i>Cyclotrachelus seximpressus</i>	0.03	0	0	0	5	P	L
<i>Cyclotrachelus sodalis</i>	51.10	11.88	58.80	4.25	11,121	P	L
<i>Dicaelus elongatus</i>	0.28	0	0	0	43	P	A
<i>Dyschirius globosus</i>	0	0	0.03	0	1	P	A
<i>Elaphropus anceps</i>	0.20	0.28	0	0.39	61	P	A
<i>Galerita janus</i>	0.03	0	0	0	4	P	A
<i>Geopinus incrassatus</i>	0	0	4.96	0	140	P	A
<i>Harpalus affinis</i>	0	0.43	0.07	0.08	36	P	A
<i>Harpalus caliginosus</i>	0.28	0	0.04	0.03	44	P	A
<i>Harpalus erraticus</i>	0.01	0.01	46.37	0	1310	P	A
<i>Harpalus herbaivagus</i>	0.05	0.17	0.35	3.64	42	H	A
<i>Harpalus pennsylvanicus</i>	2.94	8.90	12.12	20.89	2267	H	L
<i>Lebia fuscata</i>	0	0.01	0	0	1	P	A
<i>Lebia</i> spp.	0.01	0	0	0	2	X	X
<i>Leptotrachelus dorsalis</i>	0.01	0	0	0	1	X	X
<i>Poecilus chalcites</i>	18.91	61.39	4.47	8.88	7806	P	A
<i>Poecilus lucublandus</i>	5.90	0.72	1.31	6.62	1254	P	A
<i>Pterostichus commutabilis</i>	0.01	0.08	0.25	0	14	X	A
<i>Pterostichus femoralis</i>	0.04	0	0	0	6	X	X
<i>Pterostichus melanarius</i>	0.07	2.96	16.27	0.10	688	P	L
<i>Pterostichus permundus</i>	13.13	4.67	0.25	0.80	2380	P	L
<i>Scarites quadriceps</i>	4.88	0.98	0.82	0.23	847	P	A
<i>Stenolophus comma</i>	0.04	0.97	2.45	0	145	P	A
<i>Stenolophus lecontei</i>	0.01	0	0	0	1	P	A
<i>Stenolophus ochropezus</i>	0.03	0	0	0	5	P	A
<i>Stroluphus chropezus</i>	0.01	0	0	0	1	P	A
<i>Synuchus impunctatus</i>	0	0.01	0.07	0	3	P	A
<i>Trechus quadristriatus</i>	0.00	0.37	0.00	0	27	P	L
Unknown 1	0	0.01	0.07	0	2	X	X
Unknown 2	0	0	0.04	0	3	X	X
Unknown 3	0	0	0.04	0	1	X	X
Unknown 4	0.01	0	0	0	1	X	X
Unknown 5	0.01	0	0	0	1	X	X

<sup>a</sup> Carabidae are classified by trophic level as either H for herbivorous, P for predatory or omnivorous, or X for unknown.

<sup>b</sup> Carabidae are classified by overwintering stage as either A for adult, H for larva, or X for unknown.

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 calculated partial correlations for all variables in models with more than one predictor. Partial correlations were used to assess the importance of individual independent variables after adjusting for additional variables in the model. The  $AIC_c$  analysis and adjusted  $r^2$  were determined using R version 2.1.1 (R Development Core Team, 2005). Partial correlations were obtained using PROC CANCORR in SAS v. 9.1 (SAS Institute, 1999). All Carabidae variables and Opiliones were  $\log(x + 1)$  transformed, and the mean number of Araneae and Lycosidae were square root  $(x + 0.5)$  transformed prior to analysis to meet the assumptions of normality and homogeneity of variances (SAS Institute, 1999).

While no combinations of sites had an overlapping 3.5 km landscape buffer within a given year, sites did have overlapping buffers across years. Therefore, prior to interpreting the results of the  $AIC_c$  analysis, we examined potential spatial autocorrelation of the residuals of the best-fit model for each response variable between each site and the nearest neighboring site using Moran's  $I$  statistic. We did not find evidence of spatial autocorrelation for the response variables Carabidae, Carabidae diversity, adult overwintering, larval overwintering, Araneae, or Linyphiidae. We did find significant spatial autocorrelation for both Lycosidae (Moran's  $I$  statistic = 0.45,  $P = 0.033$ ) and Opiliones (Moran's  $I$  statistic = 0.50,  $P = 0.021$ ) between neighboring sites for the best-fit model. Therefore, these models and competing models were re-analyzed using a Spatial Gaussian covariance structure to account for the spatial structure present within these data. The  $P$ -values indicated in Table 3 reflect this re-analysis.

### 3. Results

#### 3.1. Activity density in soybean fields

A total of 29,300 carabid individuals comprising 62 species were collected from 26 soybean fields in 2005 or 2006 across the 4-state study region (Table 1). The total number Carabidae collected by state was 15,259 (IA), 7232 (MI), 3988 (MN) and 2821 (WI). The majority of these species were predators or omnivores (91.6%) that overwinter as larvae (56%) (Table 1). Overall, the most abundant species was *Cyclotrachelus sodalis*, which was most abundant in soybean during late June to early July followed by *Poecilus chalcites* (Say) which was most abundant from mid June to mid July (Appendix 3). Other abundant species included *Pterostichus permundus*, *Harpalus pensylvanicus*, *Harpalus erraticus*, *Poecilus lucublandus*, *Scarites quadriceps*, and *Pterostichus melanarius* (Table 1). A total of 3215 Araneae and 9058 Opiliones were collected in pitfall traps. The total number Araneae collected by state was 1230 (IA), 1327 (MI), 124 (MN), and 534 (WI). The total number Opiliones collected by state was 1874 (IA), 1661 (MI), 2291 (MN), and 3231 (WI). In both 2005 and 2006 Araneae activity density peaked in late June (Appendix 4). Eight families were found; Lycosidae was the most abundant followed by Linyphiidae (Table 2, Appendix 4). Nine species of Lycosidae were collected; the most abundant were *Trochosa terricola* and *Parsoda milvini* (Table 2).

#### 3.2. Landscape diversity

The landscape surrounding each of our field sites varied from agriculturally-dominated to forest and grassland-dominated. Within the 3.5 km landscape radius surrounding each of the 26 sites, landscape diversity values ( $D$ ) ranged from 2.43 to 6.40. The percentage of the landscape composed of annual cropland ranged from 19% to 91%. Landscapes with high and low percentages of annual cropland were present in each state (Michigan 19–91%,

**Table 2**

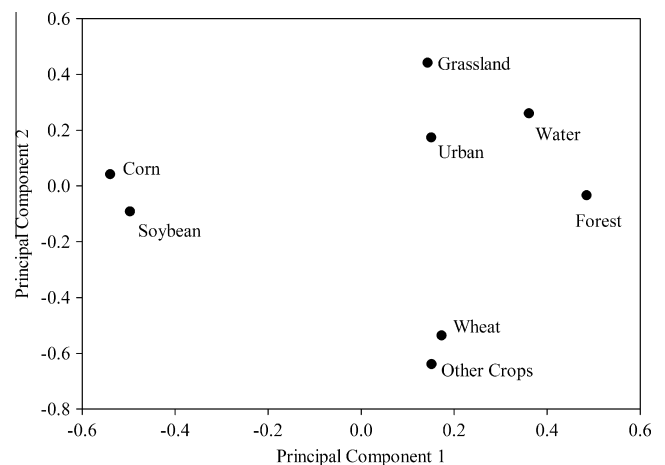
Spider community collected in pitfall traps within Iowa, Michigan, Minnesota, and Wisconsin soybean fields. All spiders were identified to family, Lycosidae were identified to genus and where possible, species.

Family	IA	MI	MN	WI
Percentage of total Araneae				
Agelenidae	0.25	0.23	2.42	2.81
Araneidae	0	0.15	0	0
Gnaphosidae	0.98	0.30	1.61	0.56
Linyphiidae	2.66	28.33	53.23	34.27
Lycosidae	88.77	66.31	40.32	61.42
Oxyopidae	0.25	0	0	0
Salticidae	0.45	1.66	0	0.37
Tetragnathidae	0	0.23	0	0
Thomisidae	6.66	2.79	2.42	0.56
Lycosidae species				
Percentage of total Lycosidae				
<i>Allocosa modesta</i>	0.18	0.34	0	0
<i>Hogna helluo</i>	4.37	1.36	0	1.22
<i>Pardosa milvini</i>	26.55	34.09	0	21.65
<i>Pardosa</i> sp. 1	0	2.61	0	0
<i>Pardosa</i> sp. 2	0	0	0	3.05
<i>Schizocosa avaida</i>	6.53	3.64	80.00	3.96
<i>Schizocosa crassipes</i>	27.06	0.23	0	4.57
<i>Trochosa terricola</i>	0.97	25.00	8.00	35.98
<i>Varacosa avara</i>	0.64	0.11	2.00	0
Immature	31.75	30.45	10.00	29.27
Damaged	1.94	2.16	0	0.30

Wisconsin 29–71%, Minnesota 44–84%, and Iowa 27–89%). At a 3.5 km radius grassland habitat comprised 1–68% (Michigan 3–19%, Wisconsin 4–20%, Minnesota 6–19%, and Iowa 5–69%) while forested habitat comprised 0–58% of the landscape surrounding field sites (Michigan 3–32%, Wisconsin 3–42%, Minnesota <1–16%, and Iowa 0–6%).

#### 3.3. Principal component analysis of landscape variables

Both principal components can be interpreted as intensity of landscape disturbance, with high values indicating less disturbed grassland and forested habitats and low values indicating greater agricultural disturbance (Fig. 1). Sites with positive loadings on PC1 were correlated with the variable Forest while negatives loadings on PC1 were correlated with the variables corn and soybean. Sites with positive loadings on PC2 were correlated with the variable grassland while negative loadings on PC2 were correlated with the variables other crops and wheat.



**Fig. 1.** PCA ordination for principal components 1 and 2 of landscape elements surrounding soybean fields sampled. Data for a radius of 2 km is shown, plots are similar for all spatial scales. Sites with positive loadings on PC1 were correlated with the variable forest while negatives loadings on PC1 were correlated with the variables corn and soybean. Sites with positive loadings on PC2 were correlated with the variable grassland while negative loadings on PC2 were correlated with the variables other crops and wheat.

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. 3). 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 forage, pastures, old fields, and in some sites small patches of restored prairie. Sites with negative values had a high proportion of locally important fruit, vegetable, ornamental, and small grain crops (Fig. 1).

### 3.4. Activity density and landscape variables

The PC2 models with the best predictors of Carabidae activity density at all six spatial scales examined; the PC2 model at 1 km had the lowest AIC<sub>c</sub> score indicating that it was the best-fit model. The intercept model was a competing model at 1 km (Table 3). A marginally-significant negative correlation was detected between Carabidae and PC2 ( $P = 0.04$ ,  $r^2 = 0.16$ ), indicating that activity density was reduced in soybean fields surrounded by an abundance of grasslands at the 1 km scale compared to landscapes dominated by other regionally important crops and wheat (Fig. 2).

When ground beetles were analyzed by overwintering stage, differences were found in their response to landscape variables. However, these differences appear to be species-specific and not necessarily shared among adult or larval overwintering taxa. The activity density of ground beetles overwintering as adults was best predicted by the PC2 model at all spatial scales except a radius of 2.5 km where the full model PC1 + PC2 + Diversity had the lowest AIC<sub>c</sub> value. The PC2 model at a radius of 1 km had the lowest AIC<sub>c</sub> value across scales (Table 3). Competing models at 1 km included PC1 + PC2 + D, and PC1 + PC2. Adult overwintering beetles were significantly negatively correlated with PC2 ( $P < 0.0001$ ,  $r^2 = 0.57$ ), indicating that their activity density in soybean fields was greater in landscapes with an abundance of wheat and other regionally important crops compared with landscapes dominated by grassland (Fig. 2). However, when individual adult overwintering species were examined, not all were negatively correlated with PC2. The two most abundant species collected, *Poecilus chalcites* and

*Harpalus erraticus* appear to be driving this pattern, exhibiting a negative relationship with PC2 at 1 km (*P. chalcites*:  $P = 0.02$ ,  $r^2 = 0.21$ , *H. erraticus*:  $P = 0.01$ ,  $r^2 = 0.22$ ) (Fig. 2). The third and fourth most abundant species (*P. lucublandus* and *S. quadriceps*) were not significantly correlated with PC2.

The activity density of ground beetles overwintering as larvae was also best predicted by the PC2 model at all spatial scales; the PC2 model at a radius of 2.5 km had the lowest overall AIC<sub>c</sub> value (Table 3). Competing models included PC2 + D and PC1 + PC2. Unlike adult overwintering beetles, the activity density of larval overwintering species was significantly positively correlated with PC2 ( $P = 0.01$ ,  $r^2 = 0.23$ ). The activity density of these species increased in soybean fields in landscapes surrounded by an abundance of grassland compared with landscapes with significant amounts of wheat and regional crops (Fig. 2). When individual species were examined patterns of activity density with PC2 varied. The most abundant species of larval overwintering ground beetle, *C. sodalis*, increased with PC2 at 2.5 km ( $P = 0.01$ ,  $r^2 = 0.23$ ) (Fig. 2). The second, third and fourth most abundant larval overwintering ground beetles (*P. permundus*, *H. pensylvanicus*, and *P. melanarius*) were not significantly correlated with PC2.

Across the sites sampled, Carabidae diversity (D) ranged from 1.21 to 2.61. Carabidae diversity was best predicted by the PC2 model at all spatial scales examined; this model had the lowest AIC<sub>c</sub> score at 2.5 km. PC2 + D was a competing model at all spatial scales. Carabidae diversity was positively correlated with PC2, indicating that the diversity of carabids found in soybean fields is greater within grassland-rich landscapes (Table 3 and Fig. 2).

For overall spider activity density, the PC1 + PC2 model had the lowest AIC value at all six scales examined. The PC1 + PC2 model at a radius of 1.5 km had the lowest AIC value across scales. PC1 was a competing model at this scale (Table 3). Spider activity density increased with both PC1 and PC2. This relationship was significant for PC1, indicating increased activity density in soybean fields in landscapes surrounded by an abundance of forested habitat (Fig. 3).

When the two most abundant families of spiders, Lycosidae and Linyphiidae were examined, Linyphiidae had a stronger correlation with landscape variables. The activity density of Lycosidae was

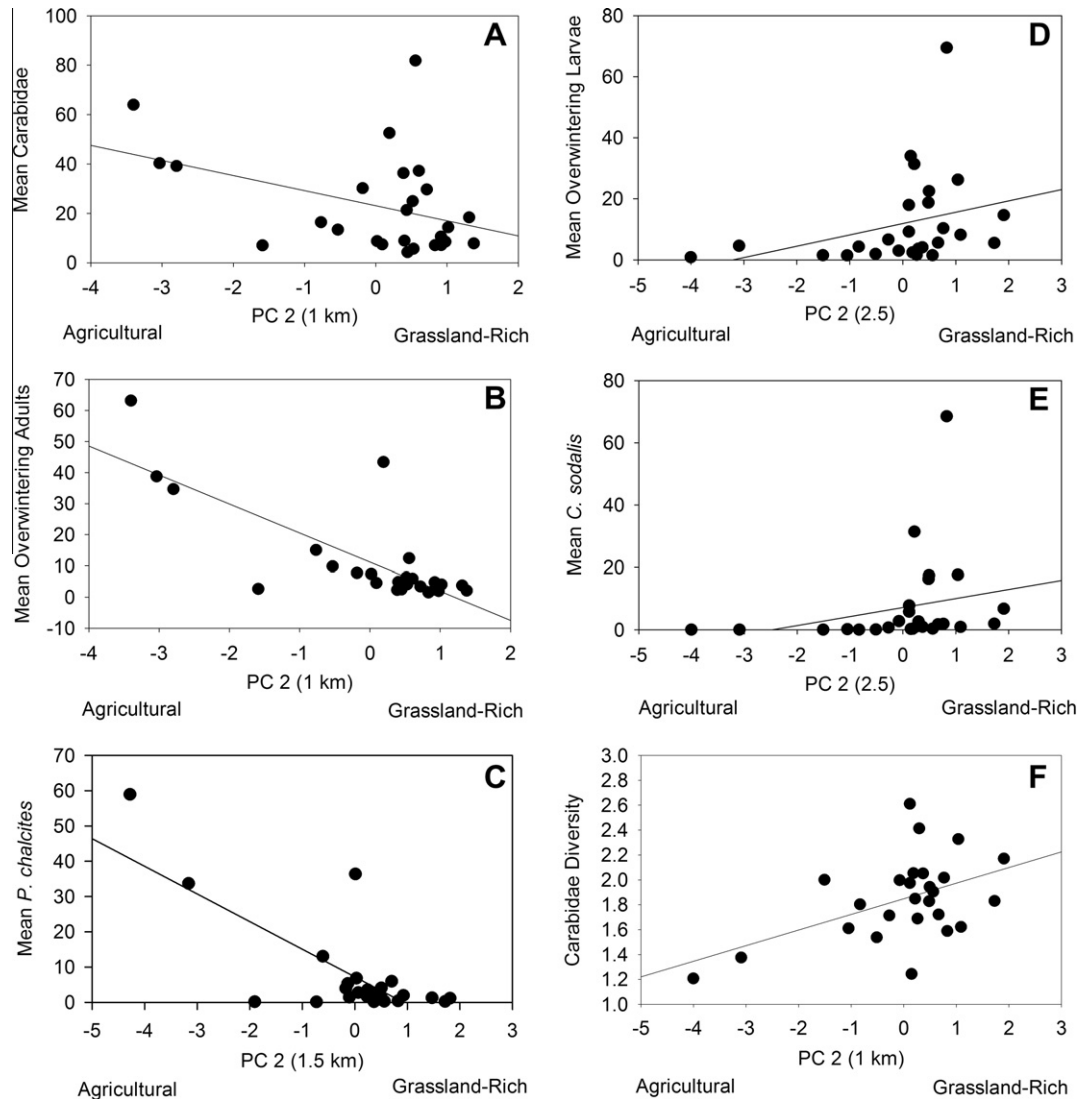
**Table 3**

Summary of model selection statistics for evaluating the activity density of Carabidae, adult overwintering Carabidae, larval overwintering Carabidae, predatory Carabidae, Araneae, Lycosidae, and Linyphiidae. The first model listed for each response variables is printed in bold and represents the minimum AIC<sub>c</sub> model. Only models with a  $A_i$  of 2 or less at the spatial scale of the minimum AIC<sub>c</sub> model are included as competing models.

Response	Radius (km)	Model <sup>a,b</sup>	Log-likelihood	$K_i$	AIC <sub>c</sub>	$\Delta_i$	$W_i$	Model $r^2$	Partial correlations
<i>Carabidae variables</i>									
All Carabidae	<b>1.0 km</b>	<b><math>B_0 + B_1</math> (PC2)*</b>	<b>-27.83</b>	<b>3</b>	<b>62.74</b>	<b>0.00</b>	<b>0.39</b>	<b>0.16</b>	
All Carabidae	1.0 km	$B_0$	-30.10	2	64.72	1.98	0.15	-	
Adult overwintering	<b>1.0 km</b>	<b><math>B_0 + B_1</math> (PC2)***</b>	<b>-23.08</b>	<b>3</b>	<b>53.24</b>	<b>0.00</b>	<b>0.47</b>	<b>0.57</b>	
Adult overwintering	1.0 km	$B_0 + B_1$ , (PC1) + $B_2$ (PC2)** + D	-20.89	5	54.78	1.54	0.22	0.64	PC1 = -0.39, PC2 = -0.59, D = 0.34
Adult overwintering	1.0 km	$B_0 + B_1$ (PC1) + $B_2$ (PC2)	-22.49	4	54.90	1.66	0.20	0.59	PC1 = -0.21, PC2 = -0.76
Larval overwintering	<b>2.5 km</b>	<b><math>B_0 + B_1</math> PC2*</b>	<b>-32.89</b>	<b>3</b>	<b>72.86</b>	<b>0.00</b>	<b>0.45</b>	<b>0.23</b>	
Larval overwintering	2.5 km	$B_0 + B_1$ PC2* + $B_2$ (D)	-32.30	4	74.52	1.66	0.20	0.27	PC2 = 0.45, D = -0.21
Larval overwintering	2.5 km	$B_0 + B_1$ (PC1) + $B_2$ PC2*	-32.34	4	74.60	1.74	0.19	0.27	PC1 = -0.20, PC2 = 0.49
Carabidae diversity	<b>2.5 km</b>	<b><math>B_0 + B_1</math> PC2*</b>	<b>-4.15</b>	<b>3</b>	<b>15.74</b>	<b>0.00</b>	<b>0.42</b>	<b>0.24</b>	
	2.5 km	$B_0 + B_1$ PC2* + $B_2$ D	-3.48	4	16.40	0.66	0.30	0.27	PC2 = 0.52, D = 0.22
<i>Arachnid variables</i>									
All Araneae	<b>1.5 km</b>	<b><math>B_0 + B_1</math> PC1* + <math>B_2</math> PC2</b>	<b>-16.19</b>	<b>4</b>	<b>42.30</b>	<b>0.00</b>	<b>0.42</b>	<b>0.35</b>	<b>PC1 = 0.52, PC2 = 0.39</b>
All Araneae	1.5 km	$B_0 + B_1$ PC1*	-18.3	3	43.68	1.38	0.21	0.24	
Lycosidae	<b>3.0 km</b>	<b><math>B_0 + B_1</math> PC2*</b>	<b>-18.87</b>	<b>3</b>	<b>44.82</b>	<b>0.00</b>	<b>0.33</b>	<b>0.14</b>	
Lycosidae	3.0 km	$B_0 + B_1$ PC1 + $B_2$ PC2*	-18.10	4	46.12	1.30	0.17	0.19	PC1 = 0.24, PC2 = 0.38
Lycosidae	3.0 km	$B_0$	-20.82	2	46.16	1.34	0.17	-	
Lycosidae	3.0 km	$B_0 + B_1$ PC2* + $B_2$ D	-18.44	4	46.80	1.98	0.12	0.17	PC2 = 0.40, D = 0.18
Linyphiidae	<b>3.5 km</b>	<b><math>B_0 + B_1</math> PC1***</b>	<b>-5.56</b>	<b>3</b>	<b>18.20</b>	<b>0.00</b>	<b>0.60</b>	<b>0.44</b>	
All Opiliones	<b>3.5 km</b>	<b><math>B_0 + B_1</math> PC1 + <math>B_2</math> (D)*</b>	<b>-32.35</b>	<b>4</b>	<b>74.62</b>	<b>0.00</b>	<b>0.37</b>	<b>0.22</b>	<b>PC1 = 0.42, D = -0.46</b>
All Opiliones	3.5 km	$B_0$	-35.58	2	75.68	1.06	0.22	-	

<sup>a</sup> \* Indicates a variable was significant  $P < 0.05$ , \*\* at  $P < 0.01$ , \*\*\*  $P < 0.001$ .

<sup>b</sup> Variables in parentheses indicate a negative relationship.



**Fig. 2.** Relationship between (A) activity density of Carabidae and PC2 at 1 km, (B) adult overwintering Carabidae and PC2 at 1 km, (C) *P. chalcites* and PC2 at 1.5 km, (D) larval overwintering Carabidae and PC2 at 2.5 km, (E) *C. sodalis* and PC2 at 2.5 km, and (F) Carabidae diversity (D) and PC2 at 1 km. Carabidae data were collected using pitfall traps. Actual means for all response variables are presented; these data (with the exception of Carabidae diversity (D)) were  $\log(x + 1)$  transformed prior to analysis.

best predicted by the PC2 model which had the lowest AIC<sub>c</sub> value at all spatial scales; the PC2 model at a radius of 3 km had the lowest AIC<sub>c</sub> value overall. There was a positive, significant correlation between PC2 and the activity density of Lycosidae ( $P = 0.02$ ,  $r^2 = 0.14$ ) (Fig. 3). Competing models at 3 km included the PC1 + PC2, intercept only, and PC2 + D models. For Linyphiidae activity density, the PC1 model had the lowest AIC<sub>c</sub> value at all spatial scales, the PC1 model at a radius of 3.5 km had the lowest AIC<sub>c</sub> value overall. No competing models were found for Linyphiidae. There was a significant positive correlation between the Linyphiidae and PC1 ( $P = 0.0002$ ,  $r^2 = 0.44$ ), indicating greater activity density in soybean fields surrounded by landscapes with an abundance of forested habitat compared with landscapes dominated by corn and soybean fields.

The activity density of Opiliones was best predicted by the PC1 + D model at 3.5 km, having the lowest AIC<sub>c</sub> value across all scales examined. The intercept only model was a competing model at 3.5 km. There was a significant negative correlation with D ( $P = 0.03$ ) indicating that highly heterogeneous landscapes supported fewer Opiliones than homogeneous landscapes (Fig. 3). These arthropods were also found more abundantly in soybean

fields within forested versus agricultural landscapes. At spatial scales of 1–3 km the intercept only model had the lowest AIC<sub>c</sub> value for Opiliones.

#### 4. Discussion

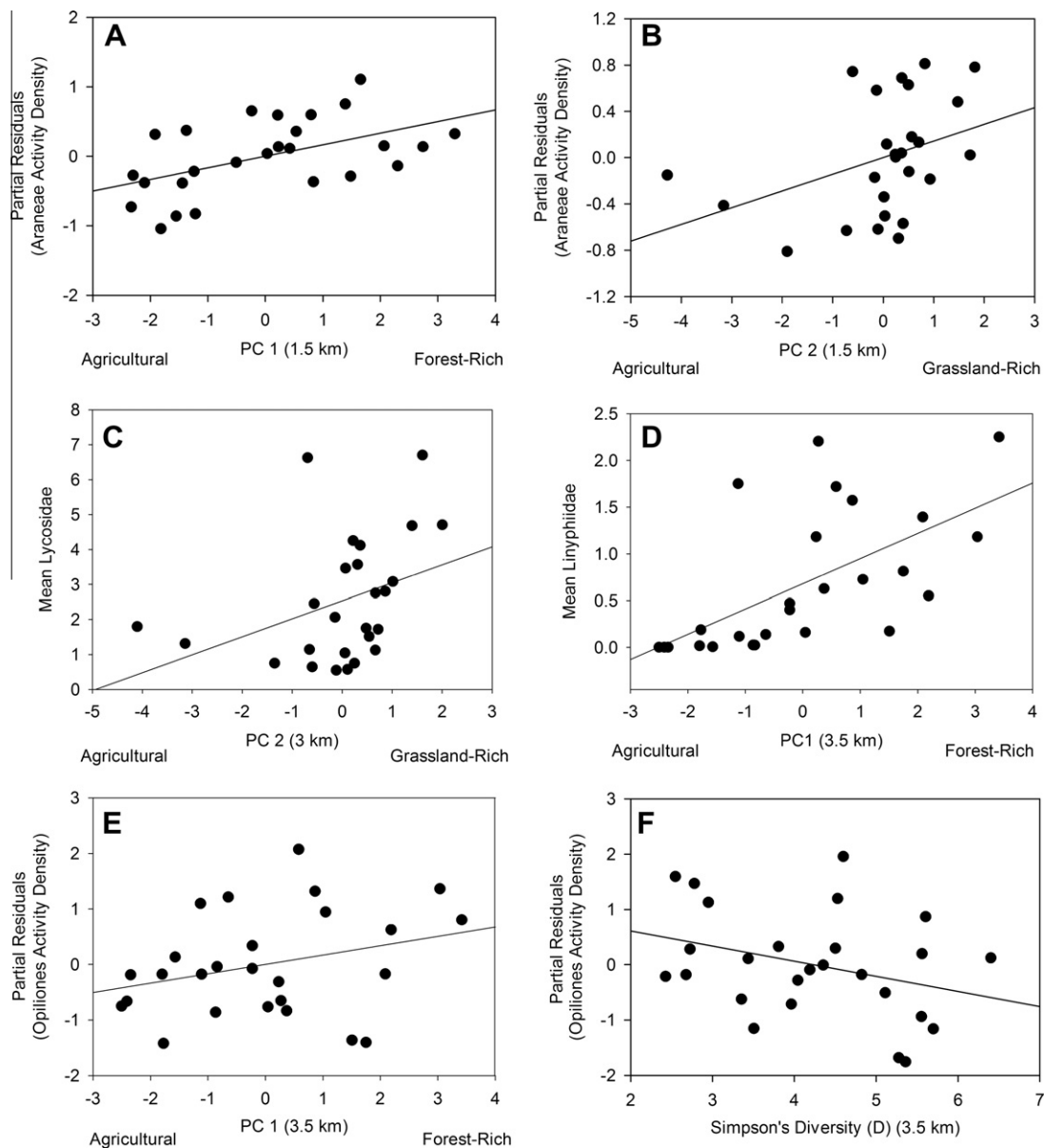
A diverse community of Carabidae and Araneae were detected in soybean fields across Iowa, Michigan, Minnesota, and Wisconsin, with 62 species of Carabidae and eight families of Araneae (nine species of Lycosidae) collected in pitfall traps from 26 sites in 2005 and 2006. The number of carabid species found throughout our study region was similar to that found by Hajek et al. (2007), however the relative abundance of taxa varied. In the Hajek et al. (2007) study the non-native species *Agrognom muelleri* was the most abundant carabid collected in New York; this species was not present in our collections. We examined three hypotheses related to the response of these ground-dwelling arthropods to the surrounding landscape. Our first hypothesis was that the activity density of Carabidae, Araneae, and Opiliones in soybean increases with the proportion of semi-natural habitats in the landscape.

We found variation in the response of these taxa to landscape composition. The activity density of Araneae supported this hypothesis, increasing in soybean fields in landscapes with an abundance of forests and grasslands. Relationships to landscape varied for Carabidae, with adult overwintering species increasing, and larval overwintering species declining with the abundance of grassland in the landscape.

#### 4.1. Relationships between carabid phenology and landscape composition

Our data did not support our second hypothesis that carabid species which overwinter as adults would be positively correlated with the abundance of semi-natural habitat in the landscape. Instead we found that relationships between landscape variables were taxon-specific and not necessarily shared among adult or

larval overwintering species. The adult overwintering species *P. chalcites*, exhibited a greater activity density in soybean fields in agriculturally-dominated landscapes, while the larval overwintering *C. sodalis* had a greater activity density in soybean fields in landscapes with an abundance of grassland patches. Schmidt et al. (2008) postulate that while many studies illustrate an increase in the abundance of habitat generalists with the proportion of semi-natural habitat, the metapopulation dynamics of these species are often complex and the response of a particular species to different habitats in the surrounding landscape may be positive or negative depending on its success in the focal habitat of study. Their hypothesis states that species that are well adapted to the focal habitat, in this case a soybean field, will respond negatively to different habitats in the surrounding landscape. Alternatively, species that are better adapted to habitats other than the focal habitat will increase with the amount of this different habitat in the land-



**Fig. 3.** Araneae activity density in 26 soybean fields was best explained by a model containing both PC1 (A) and PC2 (B) at a radius of 1.5 km. Partial residual plots of the relationship between mean spider activity density per pitfall trap and PC1 + PC2 illustrate a positive correlation with both PC1 and PC2. Plots (C and D) illustrate the relationship between Lycosidae activity density and PC2 at 3 km, and the relationship between Linyphiidae activity density and PC1 at 3.5 km respectively. Plots (E and F) illustrate the relationship between Opiliones activity density, PC1 and Landscape diversity (D). Actual means for all response variables are presented; these variables were  $\log(x + 1)$  or square root  $(x + 0.5)$  transformed prior to analysis.

scape matrix. This would suggest that *P. chalcites*, which is thought of as agricultural specialist (Larsen et al., 2003), is better adapted to agriculturally-dominated landscapes while *C. sodalis*, will favor perennial-dominated habitats including grasslands (Larsen et al., 2003).

#### 4.2. Araneae and landscape composition

Araneae had greater activity density in soybean fields in landscapes with an abundance of grassland and forested patches. Semi-natural habitat patches also influenced the activity density of the two most numerous Araneae families collected; Lycosidae and Linyphiidae. The activity density of Lycosidae exhibited a positive correlation with PC2, indicating the abundance of lycosids was greater in soybean fields in landscapes with an abundance of grassland patches. Linyphiidae activity density responded strongly to PC1, increasing in soybean fields in landscapes with an abundance of forested patches. Forested habitat was also an important variable in explaining spider species richness and species composition in oilseed rape fields (Drapela et al., 2008). Overall landscape heterogeneity has also been correlated with spider richness and abundance in wheat fields (Clough et al., 2005; Schmidt et al., 2005a; Schmidt and Tscharrntke, 2005). A stronger response to landscape by Linyphiidae compared with Lycosidae has been documented in other systems. Oberg et al. (2007) found that the activity density of Lycosidae in cereal fields was not related to landscape variables while the activity density of Linyphiidae was positively correlated to perennial crops in the surrounding landscape.

#### 4.3. Spatial scale and the dispersal of ground-dwelling predators

Our final hypothesis was that the spatial scale at which an organism responds to landscape would be a function of its capacity for dispersal, thus those that disperse mainly by walking would respond at a smaller scale compared with groups known to frequently utilize flight or ballooning. Carabidae and adult Lycosidae and Opiliones frequently colonized croplands on the ground (Drapela et al., 2008) thus we expected that these groups would respond to a smaller landscape scale compared with the Linyphiidae which frequently balloon throughout their life cycle (Bell et al., 2005). We found some support for this hypothesis with Carabidae responding at smaller spatial scales compared with the ballooning Linyphiidae. The negative response in activity density of all Carabidae and adult overwintering Carabidae was strongest at spatial radii of 1–1.5 km. Carabidae overwintering as larvae responded positively to grassland abundance at a larger spatial scale of 2.5 km. Among spider variables, the response of Lycosidae to the abundance of forested habitats was maximized at 3 km, however AIC<sub>c</sub> values of the best candidate model at each scale were very similar. The response of Linyphiidae increased with spatial scale. Since the positive correlation between Linyphiidae and PC1 was strongest at 3.5 km, our largest spatial scale measured it is possible that these species respond at even larger landscape scales.

#### 4.4. Implications

How arthropods respond to landscape composition is a function of habitat use and dispersal ability. The distribution and abundance of semi-natural and agricultural habitats within the landscape is likely to greatly influence landscape scale metapopulation dynamics of habitat generalists. It is thought that many agriculturally-important organisms following a bidirectional movement (Gavish-Regev et al., 2008), moving into agricultural fields when prey populations emerge and back into semi-natural areas in the fall when crops are harvested. While Carabidae and Araneae are known to routinely cross boundaries from semi-natural habitat

patches into agricultural crops (French et al., 2001) why they do so is vastly understudied. It is likely that some species exhibit bidirectional movement, moving into soybean from semi-natural habitats in response to prey availability. Alternatively, species may be exhibiting negligible movement (Gavish-Regev et al., 2008) through agricultural habitats, where individuals move through an unsuitable habitat to colonize other patches of suitable habitat (Gavish-Regev et al., 2008). A reduction in semi-natural habitat may force species to disperse through soybean to colonize isolated patches of preferred habitat. Understanding how habitat generalists that vary in their capacity for dispersal utilize agricultural habitats has implications for biological control as well as the conservation of biodiversity. With this information, we can expand our understanding of the functioning of these organisms at the landscape scale.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocontrol.2010.06.008.

#### References

- Bell, J.R., Bohan, D.A., Shaw, E.M., Weyman, G.S., 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research* 95, 69–114.
- Bommarco, R., 1998. Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity. *Ecological Applications* 8, 846–853.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information – Theoretic Approach*. Springer, New York.
- Clough, Y., Kruess, A., Kleijn, D., Tscharrntke, T., 2005. Spider diversity in cereal fields: comparing factors at local, landscape, and regional scales. *Journal of Biogeography* 32, 2007–2014.
- Colunga-García, M., Gage, S.H., Landis, D.A., 1997. Response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. *Environmental Entomology* 26, 797–804.
- den Belder, E., Elderson, J., van den Brink, W.J., Schelling, G., 2002. Effect of woodlots on thrips density in leek fields: a landscape analysis. *Agriculture Ecosystems & Environment* 91, 139–145.
- Drapela, T., Moser, D., Zaller, J., Frank, T., 2008. Spider assemblages in winter oilseed rape affected by landscape and site factors. *Ecography* 31, 254–262.
- Elliott, N.C., Kieckhefer, R.W., Lee, J.H., French, B.W., 1999. Influence of within-field and landscape factors on aphid predator populations in wheat. *Landscape Ecology* 14, 239–252.
- French, B.W., Elliott, N.C., Berberet, R.C., Burd, J.D., 2001. Effects of riparian and grassland habitats on ground beetle (Coleoptera: Carabidae) assemblages in adjacent wheat fields. *Environmental Entomology* 30, 225–234.
- Gardiner, M.M., Landis, D.A., Gratton, C., Schmidt, N.P., O'Neal, M., Mueller, E.D., Chacon, J., Heimpel, G.E., DiFonzo, C.D., 2009a. Landscape composition influences patterns of native and exotic ladybeetle abundance. *Diversity and Distributions* 16, 1–11.
- Gardiner, M.M., Landis, D.A., Gratton, C., DiFonzo, C.D., O'Neal, M., Chacon, J., Wayo, M., Schmidt, N., Mueller, E., Heimpel, G.E., 2009b. Landscape diversity enhances biological control of an introduced crop pest in the north-central US. *Ecological Applications* 19, 143–154.



- Gavish-Regev, E., Lubin, Y., Coll, M., 2008. Migration patterns and functional groups of spiders in a desert agroecosystem. *Ecological Entomology* 33, 202–212.
- Hajek, A.E., Hannam, J.J., Nielsen, C., Bell, A.J., Lieberr, J.K., 2007. Distribution and abundance of Carabidae (Coleoptera) associated with soybean aphid (Hemiptera: Aphididae) populations in central New York. *Annals of the Entomological Society of America* 100, 876–886.
- Kaston, B.J., 1948. Spiders of Connecticut. State Geological and Natural History Survey Bulletin Number 70. Hartford, CT. 1020 p.
- Larsen, K.J., Work, T.T., Purrington, F.F., 2003. Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia* 47, 288–299.
- Lee, J.C., Menalled, F.B., Landis, D.A., 2001. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *Journal of Applied Ecology* 38, 472–483.
- Lindroth, C.H., 1968. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 5. *Opuscula Entomologica Supplementum* 33, 649–944.
- Marino, P.C., Landis, D.A., 1996. Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecological Applications* 6, 276–284.
- McCune, B., Mefford, M.J., 1999. PC-ORD, Multivariate Analysis of Ecological Data, Version 4 Computer Program, Version By McCune, B., Mefford, M.J., Gleneden Beach, Oregon.
- Oberg, S., Ekblom, B., Bommarco, R., 2007. Influence of habitat type and surrounding landscape on spider diversity in Swedish agroecosystems. *Agriculture Ecosystems & Environment* 122, 211–219.
- Ostman, O., 2002. Distribution of bird cherry-oat aphids (*Rhopalosiphum padi* (L)) in relation to landscape and farming practices. *Agriculture Ecosystems & Environment* 93, 67–71.
- R Development Core Team, 2005. R: A Language and Environment for Statistical Computing Computer Program, Version By R Development Core Team, Vienna, Austria.
- Ragsdale, D.W., McCornack, B.P., Venette, R.C., Potter, B.D., Macrae, I.V., Hodgson, E.W., O'Neal, M.E., Johnson, K.D., O'Neil, R.J., Difonzo, C.D., Hunt, T.E., Glogoza, P.A., Cullen, E.M., 2007. Economic threshold for soybean aphid (Hemiptera : Aphididae). *Journal of Economic Entomology* 100, 1258–1267.
- Ribic, C.A., Sample, D.W., 2001. Associations of grassland birds with landscape factors in southern Wisconsin. *American Midland Naturalist* 146, 105–121.
- SAS Institute, 1999. SAS/STAT Users Guide First Edition, vol. 1. Computer Program, Version By SAS Institute, Cary, NC.
- Schmidt, M.H., Tschardtke, T., 2005. Landscape context of sheetweb spider (Araneae: Linyphiidae) abundance in cereal fields. *Journal of Biogeography* 32, 467–473.
- Schmidt, M.H., Roschewitz, I., Thies, C., Tschardtke, T., 2005a. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *Journal of Applied Ecology* 42, 281–287.
- Schmidt, M.H., Thies, C., Nentwig, W., Tschardtke, T., 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography* 35, 157–166.
- Schmidt, M.H., Roschewitz, I., Thies, C., Tschardtke, T., Nentwig, W., 2005b. Spiders in Space: How landscape-wide movement of generalist predators influences local density, species richness, and biocontrol. *Second International Symposium on Biological Control of Arthropods*, Davos, Switzerland.
- Simpson, E.H., 1949. Measurement of diversity. *Nature* 163, 688.
- Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tschardtke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421–1432.
- Thies, C., Tschardtke, T., 1999. Landscape structure and biological control in agroecosystems. *Science* 285, 893–895.
- Thies, C., Steffan-Dewenter, I., Tschardtke, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101, 18–25.
- Tschardtke, T., Brandl, R., 2004. Plant–insect interactions in fragmented landscapes. *Annual Review of Entomology* 49, 405–430.
- Tschardtke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8, 857–874.
- Ubick, D. P. Paquin, P.E. Cushing, and V. Roth (Eds.). 2005. Spiders of North America, an identification manual. American Arachnological Society. 377 p.
- Weibull, A.C., Ostman, O., Granqvist, A., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation* 12, 1335–1355.
- Wiens, J.A., Schooley, R.L., Weeks, R.D., 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78, 257–264.
- Wissinger, S.A., 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biological Control* 10, 4–15.
- With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13, 314–326.
- With, K.A., Cadaret, S.J., Davis, C., 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology* 80, 1340–1353.