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Effect of aphids and the surrounding landscape on the abundance of Coccinellidae in cornfields

N.C. Elliott,[a,*] R.W. Kieckhefer,[b] and D.A. Beck[b]

[a] USDA, ARS, SPA, Plant Science Research Laboratory, 1301 N. Western St., Stillwater, OK 74075, USA
[b] USDA–ARS, Northern Grain Insects Research Laboratory, 2923 Medary Ave., Brookings, SD 57006, USA

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Abstract

We determined how the composition and patchiness of eastern South Dakota agricultural landscapes surrounding cornfields and the abundance of aphids in cornfields affected the abundance of adult coccinellids in cornfields. Four species of Coccinellidae were common in cornfields during the three-year study. Five variables describing the composition and patchiness of the landscape surrounding cornfields (% of pasture/grassland, % of wooded land, % of Conservation Reserve Program land, % of wetland, and boundary density) and abundance of aphids in the cornfields were used as predictor variables to construct stepwise multiple regression models to describe the abundance of each species of Coccinellid in the cornfields. Regression models explained for 8–45% of the variation in abundance of adult coccinellids depending on species. Abundance of aphids entered into regression models for three of the four species. The regression coefficient for aphid abundance was positive in models for two species, but was negative in the model for *C. maculata*. Each of the five landscape variables was included in a regression model for one or more coccinellid species. Results are discussed in relation to the biology and ecology of the species of Coccinellidae that inhabit cornfields in eastern South Dakota. Published by Elsevier Science (USA).

Keywords: Aphididae; Predator; Landscape structure; Agroecosystem; Aggregation; Numerical response

1. Introduction

Corn. *Zea maize* L., is an important field crop in eastern South Dakota and most of the Midwestern United States. The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), frequently infests corn and sometimes reaches high densities. Damage to corn caused by corn leaf aphids generally is not serious, but can occasionally result in severely reduced yields (Foott, 1975). Coccinellidae species are conspicuous predators of corn leaf aphids and are sometimes the most abundant predators of aphids in cornfields (Coderre and Tourneur, 1986). Evidence is contradictory concerning whether coccinellids control corn leaf aphids below economically damaging levels in corn. Foott (1973) reported from Ontario, Canada that coccinellids were unable to prevent damage to corn caused by corn leaf aphids because the density of coccinellids did not increase to sufficient levels for control until after the aphid infestation had peaked and most injury to plants had occurred. On the other hand, Coderre and Tourneur (1986) found that coccinellids substantially suppressed corn leaf aphids in corn in Quebec, Canada.

The main factors determining whether coccinellids can maintain corn leaf aphids below economically damaging densities in cornfields are temporal synchrony between coccinellid and aphid populations and the overall density of coccinellids in the field (Coderre and Tourneur, 1986; Foott, 1973; Wright and Laing, 1980). Corn leaf aphids can build to high densities inside the whorls of unexpanded corn leaves where they are protected from predation by coccinellids until the leaves expand prior to flowering. Thus, coccinellids can be inconsistent at suppressing corn leaf aphids and this is at least partially dependent on the timing of colonization of corn plants by corn leaf aphids (Coderre, 1988).

Several factors influence the abundance of coccinellids in cornfields and probably also the timing of colonization of the field by coccinellids. In addition to the

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[*] Corresponding author. Fax: +405-372-1398.
E-mail address: nelliott@pswcrl.ars.usda.gov (N.C. Elliott).

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density of aphids, the density of certain weeds in a cornfield can influence coccinellid density (Cottrell and Yeargan, 1998a), as can the abundance of corn pollen (Coderre and Tourneur, 1986; Cottrell and Yeargan, 1998b). Corn plant density can also influence coccinellid abundance (Smith, 1971).

Characteristics of the agricultural landscape in which a cornfield is embedded may also influence the abundance of coccinellids in the field, however, the role of the surrounding landscape in determining the abundance of coccinellids in cornfields has not been investigated. Studies in wheat in eastern South Dakota demonstrated an influence of landscape structure on the abundance of coccinellids. Both the composition and patchiness of the mosaic of ecosystems surrounding wheat fields were found to influence the abundance of coccinellids and the effect of the surrounding landscape on abundance differed among coccinellid species (Elliott et al., 1998). In this paper, we describe the effects of the composition and patchiness of the landscape, and the abundance of aphids, on the abundance of coccinellids in cornfields in eastern South Dakota.

2. Materials and methods

The study was accomplished in commercial cornfields in six eastern South Dakota counties: Brookings, Deuel, Hamlin, Kingsbury, Lake, and Moody (Fig. 1). To investigate the effects of aphids and landscape structure on patterns of coccinellid abundance, cornfields were selected for study from within each of the six counties each year during 1988, 1989, and 1990. A variable number of fields were chosen from within each county each year for sampling. Our criteria for field selection were to: (1) avoid sampling fields that were obviously atypical of production fields in the region; (2) avoid sampling fields in close proximity to one another; and (3) avoid sampling a particular field more than one time during the study. All sampling was done between 12 July and 12 August each year to reduce the potentially confounding effect of seasonal variation in insect populations on spatial patterns of insect abundance. In total, 26, 32, and 40 fields were sampled, respectively, in 1988, 1989, and 1990.

Adult predaceous coccinellids were sampled in fields by visual inspection of corn plants for one hour. To initiate sampling in a field, a row of corn plants was arbitrarily chosen. An observer walked down the row into the interior of the field a distance of ca. 10 m before starting to sample. The observer then walked down the row stopping at each corn plant and collecting all adult coccinellids seen into a hand-held, mouth suction, aspirator. After 15 min of sampling in the row, the observer chose a second row 10 or more rows removed from the first row and inspected plants in it for 15 min.

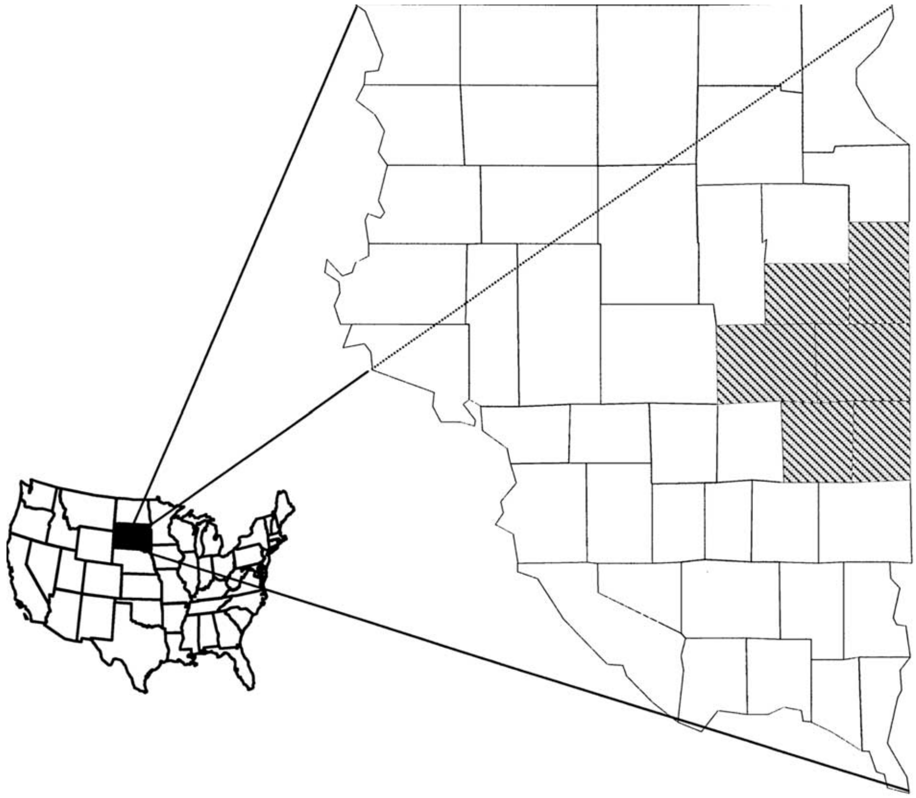

Fig. 1. The six county study area in eastern South Dakota from which 98 cornfields were arbitrarily chosen and sampled.

Four rows were sampled per field for a total of 1 h of sampling. All coccinellids were returned to the laboratory where they were identified to species. Ambient air temperature (°C), percent relative humidity, solar irradiance (w/m^2), and wind speed (m/s) were measured just prior to and just after sampling for coccinellids.

Abundance of aphids was estimated for a field at the same time coccinellids were sampled using a rating system whereby an integer value was assigned to the number of aphids on individual corn plants as follows: 0, no aphids; 1, 1–5 aphids; 2, 6–25 aphids; 3, 26–125 aphids; 4, 126–625 aphids; and 5, more than 625 aphids. Abundance of aphids was determined using the rating system on 25 corn plants selected arbitrarily from each of the four rows the observer traversed, for a total of 100 plants per field. Corn plant growth stage was measured for each of the 100 plants sampled for aphids using Hanway's rating system (Richie and Hanway, 1982). By Hanway's method, growth stage is given a value from 0.1 to 10, with 0.1 corresponding to coleoptile emergence from the soil and 10 corresponding to physiological maturity.

The composition of the landscape surrounding each field was determined from high altitude aerial panchromatic photographs obtained from the US Farm Service Agency, Brookings, SD. Each photograph covered one section ($1.6 \times 1.6\,km^2$) of land. The area of land in five land cover categories was calculated for each of the nine sections, the section containing the sampled field and the eight sections immediately surrounding the one containing the sampled field (Fig. 2). Land cover for each photograph was grouped into five categories: agricultural (cultivated) land, uncultivated land (mostly pasture and other grasslands), wooded land, USDA Conservation Reserve Program (CRP) land, and wetland. Land enrolled in the CRP is planted to grasses, but is not grazed, mowed, or burned. A small amount of the land was covered by man-made structures such as farmsteads and roads; the area of land in this category was not recorded. Land cover data were expressed as percentages of the total area of each section in a particular land cover category. The number of boundary crossings between land cover types was estimated for each section by drawing two straight lines from corner

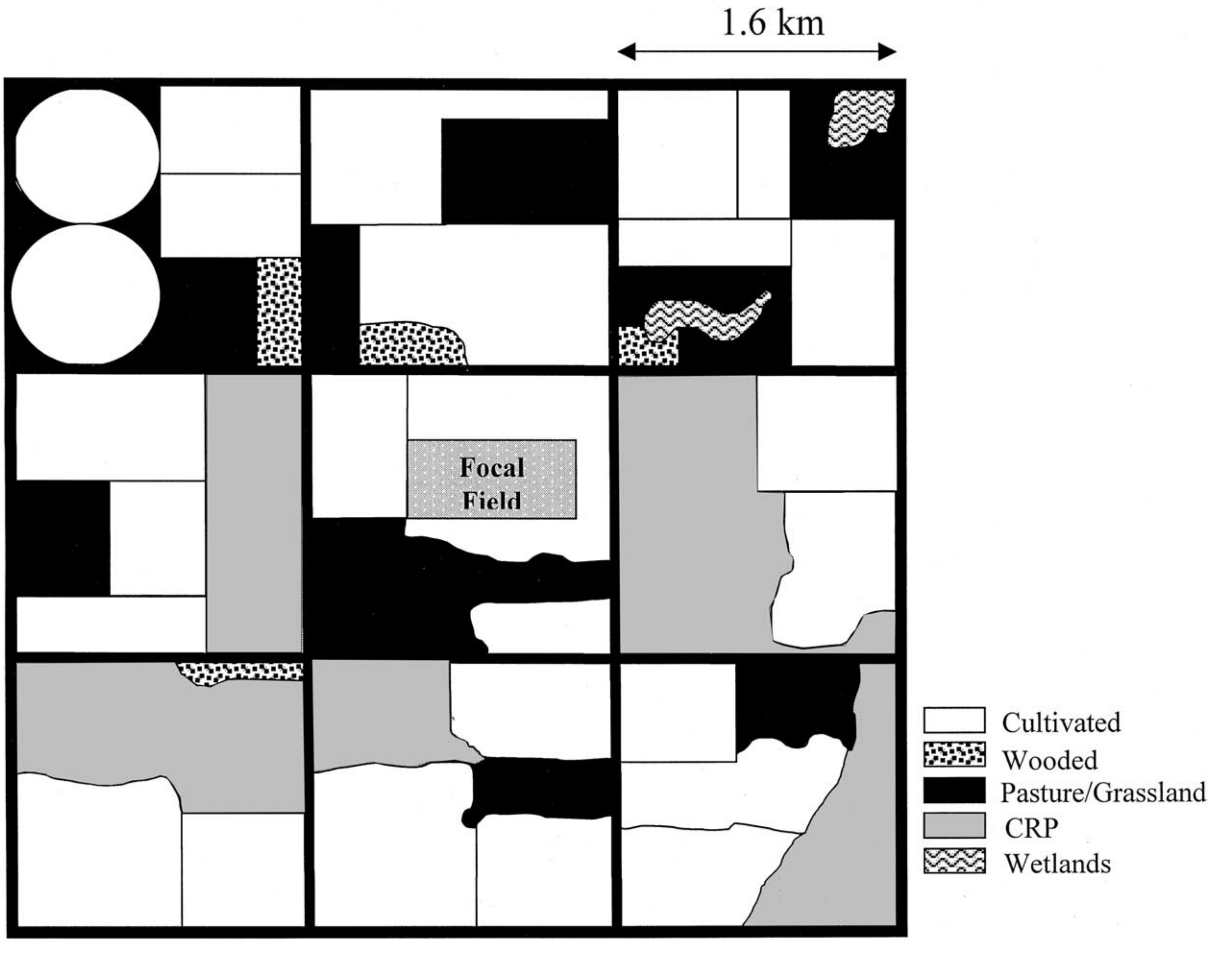

Fig. 2. A hypothetical study field and the surrounding nine sections ($1.6 \times 1.6\,km^2$) for which land cover data were recorded.

to corner across the diagonals of the photograph and counting the number of boundaries between land cover types crossed along the length of each line. The mean of the two numbers, thus, obtained was calculated and used as a measure of the average patch size for the landscape surrounding the field. For each sampled field, the mean percentage land in each land cover category and the number of boundaries crossed were calculated for the nine sections surrounding each sampled field and averaged to provide measures of landscape variability to use as predictor variables in stepwise multiple regression modeling.

Year, day of the year, and corn plant growth stage are known to exert an effect on abundance of coccinellids and aphids in cornfields (Cottrell and Yeargan, 1998a,b; Kieckhefer and Elliott, 1990), while the efficiency of visual sampling for coccinellids in some agricultural crops is influenced by meteorological variables (Michels et al., 1996). Therefore year, day of the year, and corn plant growth stage were used as covariables in regressions to adjust abundance of aphids, prior to using it as a predictor variable in stepwise multiple regression modeling for coccinellid abundance. Similarly, the abundance of each coccinellid species was adjusted for the covariables listed in Table 1 by forcing these variables into regression models, prior to undertaking the stepwise phase of regression modeling wherein adjusted abundance of aphids and the landscape variables were tested for entry as predictors in models in which the abundance of various coccinellid species were the dependent variables. *F* tests were used to determine the significance of predictor variables in regression models with α for inclusion of a predictor in a model set at 0.10. Multiple regression models were constructed using PROC REG with the MAXR option, which ensures that a model with a particular number of predictor variables has maximum R^2 among all possible models with that number of predictors (SAS Institute, 1990).

Table 1
Mean of landscape variables and covariables for 98 cornfields sampled for coccinellids during 1988, 1989, and 1990

Variable	$\bar{x}$ (range)
Abundance of aphids rating[a]	1.14 (0.0–4.70)
Landscape variables	
Percentage of grassland/pasture	17.7 (4.9–51.1)
Percentage of woods	3.1 (1.3–8.4)
Percentage of CRP[b]	6.3 (0.0–31.5)
Percentage of wetlands/water	5.8 (0.0–38.9)
Number of boundaries crossed	7.2 (3.1–10.9)
Covariables	
Corn plant growth stage[c]	4.9 (2.7–8.0)
Year	1989 (1988–1990)
Day of the year	210 (193–224)
Time of day (h)	1140 (0815–1530)
Windspeed (m/s)	3.1 (0.3–7.2)
Air temperature (°C)	26.1 (17.8–34.4)
Relative humidity (%)	60.2 (30.0–85.0)
Solar radiation (w/m^2)	1060 (175–1575)

Each observation on which the mean is based is the mean percentage for the nine sections (1.6 × 1.6 km^2) surrounding the cornfield.

[a] 0, no aphids; 1, 1–5 aphids; 2, 6–25 aphids; 3, 26–125 aphids; 4, 126–625 aphids; and 5, more than 625 aphids.

[b] USDA Conservation Reserve Program land.

[c] Hanway's rating system (Richie and Hanway, 1982).

3. Results and discussion

The composition of the landscape matrix surrounding a cornfield, and the size of patches comprising it, varied markedly among sampled cornfields in the six counties (Table 1). For example, % of pasture/grassland per section varied from a mean of 4.9 to 51.1% ($\bar{x} = 17.7\%$) for the nine sections surrounding a sampled field, while the mean number of boundaries crossed per section for the nine sections (a measure of patch size) ranged from 3.1 to 10.9 ($\bar{x} = 7.2$).

Abundance of aphids and coccinellids varied among years (Table 2). In 1988 and 1990, *Coleomegilla maculata lengi* Timberlake was the most abundant species of Coccinellidae; while *Hippodamia convergens* Guerin–Meneville was the most abundant species in 1989. *Hippodamia tredecimpunctata tibialis* (Say) and *Coccinella septempunctata* (L.) were relatively common in all years. *Hippodamia parenthesis* (Say), *Coccinella transversoguttata richardsoni* Brown, *Cycloneda munda* (Say), and *Adalia bipunctata* (L.) were found in low numbers and were grouped in a single category 'uncommon coccinellids.' Abundance of aphids also varied among years, from a mean rating of 0.01 in 1988 to 2.75 in 1989 (Table 2). Aphids in corn were predominantly corn leaf aphids, but small numbers of bird cherry-oat aphids, *Rhopalosiphum padi* (L.), also occurred.

Several landscape variables were correlated (Table 3). In particular, % of cultivated land was negatively cor-

Table 2
Mean abundance of aphids rating per corn plant (±SE) and mean number of coccinellids captured per 15 min of searching (±SE) in cornfields sampled during 1988, 1989, and 1990

	Year		
	1988 (26)	1989 (32)	1990 (40)
Abundance of aphids rating[a]	0.01 ± 0.01	2.75 ± 0.21	0.59 ± 0.05
H. convergens	2.37 ± 0.67	13.20 ± 2.79	0.74 ± 0.14
H. tredecimpunctata	0.46 ± 0.13	0.60 ± 0.21	1.87 ± 0.27
C. maculata	5.94 ± 1.48	1.21 ± 0.31	4.74 ± 0.75
C. septempunctata	0.07 ± 0.04	0.61 ± 0.10	1.68 ± 0.19
Other coccinellids	0.19 ± 0.07	0.11 ± 0.04	0.43 ± 0.16

The number of fields sampled during a year is listed in parentheses after the year.

[a] 0, no aphids; 1, 1–5 aphids; 2, 6–25 aphids; 3, 26–125 aphids; 4, 126–625 aphids; and 5, more than 625 aphids.

Table 3
Correlation coefficients among landscape variables for cornfields sampled during 1988, 1989, and 1990 ($n = 98$)

Variable	Percentage of pasture	Percentage of wooded	Percentage of wetland	Percentage of CRP	Number of boundaries
Percentage of cultivated	−0.75*	−0.39*	−0.53*	−0.58*	−0.54*
Percentage of pasture		0.31*	0.08	0.34*	0.50*
Percentage of wooded			−0.04	0.34*	0.38*
Percentage of wetland				−0.17	0.13
Percentage of CRP[a]					0.36*

Each observation for a particular landscape variable is the mean of the variable for the nine sections ($1.6 \times 1.6\ \text{km}^2$) containing and surrounding the sampled cornfield.

[a] USDA Conservation Reserve Program land.

related with all other landscape variables. The large negative correlations of % of cultivated land with the % of land in other land cover categories reflect the fact that cultivated land decreased in direct relation to increasing amounts of land in the other categories.

Apparently, multiple land uses tend to occur in the landscape when the amount of cultivated land is reduced, thus, accounting for the negative correlation with each land cover type. As a result of its strong negative correlation with all other landscape variables, % of cultivated land was not used in stepwise regression modeling.

Prior to stepwise regression modeling, regressions were calculated for abundance of each coccinellid species and for abundance of uncommon coccinellids against covariables listed in Table 1 to adjust for temporal variation in abundance of coccinellids. The percentage of variation in abundance of coccinellids accounted for by covariables ranged from 20 to 51% (Table 4). The five landscape variables and abundance of aphids accounted for 8 to 45% of the variation in the abundance of coccinellids in stepwise regression models (Table 4).

For most coccinellids for which abundance of aphids entered into the regression model, abundance increased with increasing abundance of aphids as indicated by positive regression coefficients (Table 4). However, the regression coefficient for abundance of aphids in the model for *C. maculata* was negative indicating that abundance of *C. maculata* decreased with increasing abundance of aphids. The relationship between abundance of *C. maculata* and abundance of aphids initially seems counterintuitive. However, the negative relationship could be the result of the pollenivorous habit of *C. maculata* (Cottrell and Yeargan, 1998b; Hodek and Honek, 1996). Density of corn leaf aphids in corn typically begins to decrease after the 'late whorl' stage (prior to anthesis) because the aphids, which prefer to inhabit the whorl, are subject to increased mortality after the last leaves unfurl (Wright and Laing, 1980). Thus, pollen-shed in corn occurs at a time when density of corn leaf aphids is typically decreasing. If *C. maculata* responds numerically to the availability of corn pollen, it would frequently increase in abundance in cornfields at a time when the density of aphids in the field was decreasing.

Landscape variables entered into multiple regression models for all coccinellid species except *C. septempunctata* and uncommon coccinellids. Among landscape variables, % of pasture/grassland entered in stepwise regression models for abundance of two coccinellid species (*H. tredecimpunctata* and *C. maculata*). The % of wooded land entered in the model for *C. maculata* and % of CRP land entered in the model for *H. convergens*. Patch size (# boundaries crossed) entered the model for abundance of *H. convergens* with a negative regression coefficient.

From the perspective of stepwise regression modeling, the existence of correlations between several landscape variables indicated that regression coefficients associated with particular landscape variables would tend to misrepresent their importance in determining the

Table 4
Stepwise multiple regression models for abundance of adult coccinellids

Coccinellid species	Predictor variables included	Contribution to R^2	
		Predictors	Covariables
H. convergens	0.30 + 0.42 × aphids + 0.02 × % of CRP[a] − 0.06 × # of boundaries crossed	0.45	0.51
H. tredecimpunctata	−0.28 + 0.02 × % of pasture/grassland − 0.01 × % of wetland/water	0.24	0.22
C. maculata	0.04 − 0.03 × % of pasture/grassland + 0.14 × % of wooded − 0.16 × aphids	0.28	0.20
C. septempunctata	−0.03 + 0.07 × aphids	0.08	0.33
Other coccinellids	None significant	—	—

Variables are listed in decreasing order of their contribution to model R^2. Model R^2 gives the contribution of all predictor variables, excluding covariables. The contribution of covariables to total R^2 is listed separately.

[a] USDA Conservation Reserve Program land.

abundance of coccinellids in cornfields whenever two or more correlated landscape variables were included in a model. When a landscape variable entered a model, the explanatory power of a correlated landscape variable on abundance of the particular coccinellid species would be reduced. However, variables would not enter in a regression model if they had no influence on the abundance of the particular species. Therefore if a landscape variable was highly correlated with another landscape variable that was already in the model its effect might be largely accounted for and, thus, another variable not as strongly correlated with the variable in the model but perhaps less influential in determining the abundance of the particular coccinellid might be incorporated in the model instead. Since only two landscape variables entered into a model for a species, a simple way to determine whether the predictors in a model were those with the greatest effect on the dependent variable was to delete the most influential landscape variable from the model, i.e., the one with the greatest contribution to R^2 and re-fit the model to determine the next most influential variable. When this was done for each species, the landscape variable that entered first in the re-fitted regression model was the same landscape variable that entered second among landscape variables in the original multiple regression model. Furthermore, the sign of the regression coefficient of the landscape variable was unchanged from that in the original model. Thus, in spite of correlation among landscape variables, the landscape variables incorporated in multiple regression models for each species (Table 4) were those that independently had the greatest influence on abundance of the particular coccinellid species.

The importance of wooded land in the regression model for *C. maculata* is probably primarily the result of its role as overwintering habitat for coccinellids. *C. maculata* and *H. tredecimpunctata* are known to overwinter primarily in wooded areas in eastern South Dakota (R.W. Kieckhefer unpublished data). The habitats utilized by *H. convergens* for overwintering in eastern South Dakota have not been identified and we suspect that the species does not normally overwinter successfully in eastern South Dakota (R.W. Kieckhefer personal observation). The importance of wooded habitat in the regression model for *C. maculata* may highlight the importance of preferred overwintering habitat in the ecology of this species in eastern South Dakota. *C. maculata* apparently disperses shorter distances than *H. convergens* (Ewert and Chiang, 1966; Elliott et al., 2000) and *C. septempunctata* (Giles et al., 1994). The inclusion of the percentage of wooded land in the regression model for *C. maculata* in this study and in a previous study in wheat (Elliott et al., 1998) indicates that the presence of wooded land near agricultural fields is particularly important in determining the local abundance of *C. maculata*. Considering the greater levels of dispersal by *C. septempunctata* and especially by *H. convergens* compared with *C. maculata*, it is reasonable to expect that the availability of habitats with essential resources near agricultural fields would be particularly important in determining the abundance of the latter species.

The influence of the landscape matrix on the local abundance of a species depends to a large extent on the composition and grain size of the landscape in relation to the species resource requirements and biological characteristics. Dispersal ability and habitat requirements are particularly important in this respect (Dunning et al., 1992; Fahrig and Merriam, 1994). For most of the Coccinellidae we studied, overwintering and breeding occur primarily in different habitats and individuals must move between habitats during the growing season to track ephemeral prey populations. In a diverse, fine-grained, landscape, individual predators may not need to travel far to obtain essential resources. In that case, the influence of patchiness in the distribution of resources on the abundance of a species would be relatively local and variation in the abundance of a species in response to spatial variation in the composition, size, and distribution of patches comprising the landscape matrix would be minimal. In a coarse-grained landscape, matrix effects on local abundance of coccinellids would be accentuated because resources would not be equally accessible to all individuals. We have shown that species of Coccinellidae are strongly influenced by variation in the composition and patchiness of the landscape surrounding cornfields, suggesting that coccinellids perceive agricultural landscapes in eastern South Dakota as coarse-grained; and the structure of the landscape partially determines the local abundance of these important biological control agents. Previous studies have shown that the abundance of coccinellids in agricultural fields is influenced by variation in landscape structure at the scale typically observed in agricultural landscapes (Colunga-Garcia et al., 1997; Elliott et al., 1998; Honek, 1982). Habitat management has considerable potential for increasing the effectiveness of natural enemies in biological control of crop pests (Landis et al., 2000). For Coccinellidae in agricultural landscapes, it may be possible to enhance populations of coccinellids in agricultural crops by manipulating the size and composition of the elements comprising the landscape matrix. Such manipulation could prove effective when undertaken at a very fine scale, but as our study shows, might also be effective when applied over kilometer wide areas.

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