Response of an Assemblage of Coccinellidae (Coleoptera) to a Diverse Agricultural Landscape

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ABSTRACT Changes in species assemblages of predatory coccinellids in response to landscape structure (habitat diversity and patchiness) was studied in a southern Michigan landscape during 1989–1990. Three sites with different mosaics of cultivated (alfalfa, corn, wheat) and uncultivated (deciduous, field succession) habitats were sampled for coccinellid species using yellow sticky traps. The landscape at each site was characterized using the Berger–Parker index for habitat diversity and a relative patchiness index for habitat fragmentation. Relative abundance, species richness, species dominance, and the Kendall coefficient were used to analyze and compare species assemblages among sites. Principal component analysis (PCA) was used to extract factor components per species and site scores, which were compared with landscape indices using the Pearson correlation coefficient. Thirteen species of coccinellids were captured during the 2 yr of weekly sampling. Of these species, *Coccinella septempunctata* (L.) was the dominant species in the landscape and was equally abundant in the 3 sites. *Coleomegilla maculata lengi* Timberlake was more abundant in the site that had a corn habitat, whereas *Cycloneda munda* (Say), *Chilocorus stigma* (Say), and *Brachiacantha ursina* (F.) were more abundant in the site that had a deciduous habitat. Overall, the site with a deciduous habitat had higher species richness. There were significant differences in species composition between the site with a deciduous habitat and the other 2 sites. Differences observed among sites were significantly correlated with the presence of uncultivated habitats in the landscape.

KEY WORDS Coccinellidae, agroecosystems, landscape structure, species diversity, habitat diversity, field crops

ECOLOGICAL PEST MANAGEMENT systems rely on a thorough understanding of the plant, herbivore, and natural enemies in agroecosystems (Altieri 1983). Although natural enemies have been used to regulate pests of agricultural crops successfully, there is still a lack of understanding of the effect of landscape structure on the population dynamics of beneficial insects beyond the boundaries of individual fields (Taylor 1990). Diversity, for instance, has been one of the important issues in studies that relate habitat structure with natural enemies. Most of these studies have focused primarily on within-field or field-edge diversity (Altieri 1994). However, agricultural activities have an impact at larger scales affecting the structure of the entire landscape and influencing communities of natural enemies (Colunga-Garcia 1996, Marino and Landis 1996). In that context, an aspect that has not been fully addressed in agroecosystem studies is the habitat diversity that results from the mosaic of patches of crop fields and uncultivated habitats and their effect on organisms. Species assemblages of insects can be affected by changes in land-use cover types (Luff and Woiwod 1995). Knowledge obtained at this scale is critical to understand the dynamics of natural enemies, which traverse the landscape searching for food, sites for reproduction, and shelter against unfavorable environmental conditions or disturbances originating from agricultural practices (Wratten and Thomas 1990). Such studies will contribute greatly to our understanding of the factors that influence dynamics of natural enemies in the landscape and will allow the redesign of agroecosystems to enhance the action of natural enemies (Dennis and Fry 1992).

Predatory coccinellids are known for the wide range of habitats they can effectively exploit by virtue of their high mobility (Kieckhefer et al. 1992, Maredia et al. 1992a). Using this group of organisms and as a step toward the study of the response of predatory insects to habitat diversity in agricultural landscapes, we formulated the following question: Does habitat arrangement in the landscape affect the assemblage of predatory coccinellids? To address this question, the current work was conducted in a selected Michigan landscape with the objective of quantifying the changes in species assemblages of predatory coccinellids in response to landscape structure characterized by habitat diversity and fragmentation.

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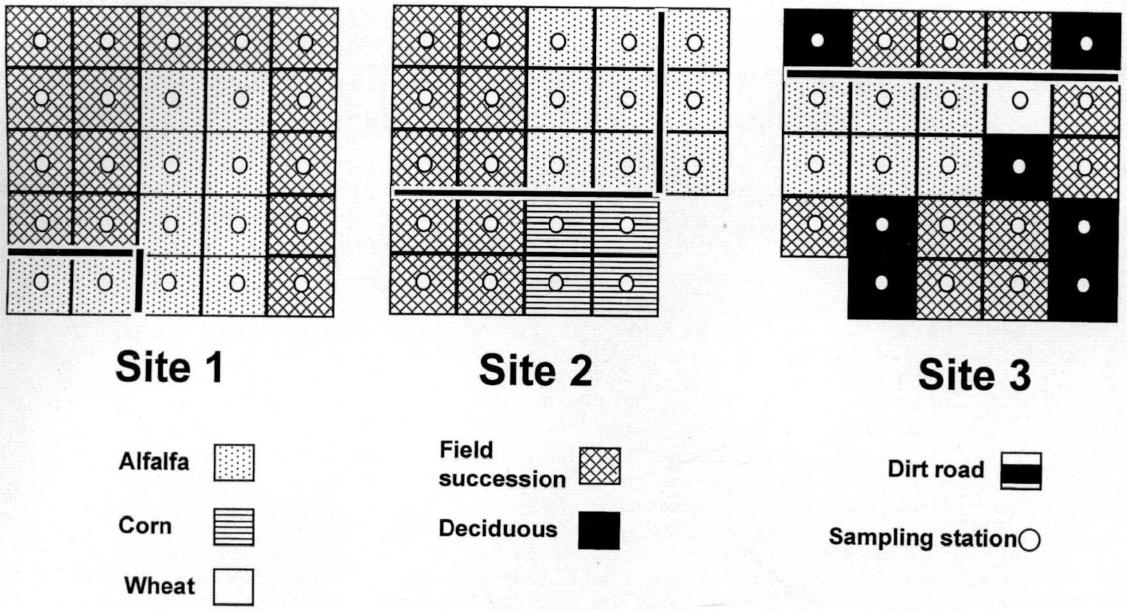

Fig. 1. Habitat distribution in 3 sites as described by the primary habitat at each quadrat (100 m^2) centroid; Kellogg Biological Station, Hickory Corners, MI; 1989–1990.

Materials and Methods

Study Area. This study was conducted at the Kellogg Biological Station, Hickory Corners, MI, where the landscape consists of early and late stages of plant succession and agricultural fields interspersed with forests, wetlands, and lakes (Burbank et al. 1992). Three sites (500 by 500 m) with a different habitat composition were selected as subsets of the landscape. The primary habitats in each site were as follows: site 1, alfalfa and field succession; site 2, alfalfa, corn, and field succession; and site 3, alfalfa, wheat, field succession, and mature deciduous forest. Field succession consisted primarily of the perennial grasses *Agropyron repens*, *Bromus inermis*, and *Phleum pratense*, with interspersed patches of *Aster pilosus*, *Daucus carota*, and *Solidago* spp. In deciduous forest, the dominant species were *Prunus serotina*, *Juglans nigra*, and *Quercus* spp.

In this article, the term "site" is used to refer to each of the 3 local landscapes in the study.

Sampling Method. Sticky traps were selected as a sampling tool because they can be placed permanently in all habitats, increasing the number of samples obtained per time unit. An increase in the number of samples increases the likelihood of capturing rare species (Southwood 1978). Trap captures have an inherent insect activity component highly influenced by existing weather conditions (Southwood 1978). However, changes caused by daily weather conditions are averaged by the constant exposure of the traps (Tollefson and Calvin 1994).

In each site, permanent sampling stations were placed 100 m apart, totaling 25, 23, and 24 stations, respectively, for sites 1, 2, and 3 (Fig. 1). Each sampling station consisted of a double-sided, cardboard yellow sticky trap (22.5 by 14.0 cm) suspended 1.2 m above the ground from a metal pole as described by Maredia et al. (1992b). Yellow cardboards were replaced every 2nd wk. Coccinellid adults caught on traps were counted, recorded, and removed every week. The duration of the sampling was from July to October in 1989 and from March to October in 1990.

Species Assemblages. Three analytical techniques were used to analyze and compare coccinellid species assemblages, as follows: (1) multiple comparisons of relative abundance, species richness, and species dominance; (2) the Kendall rank correlation test; and (3) principal component analysis.

Relative Abundance. This was measured as the average number of adults captured per trap. To minimize the effect of beetle activity in the meaning of trap captures, mean trap captures were calculated over the entire sampling period (37 wk). Use of broad time intervals (i.e., an entire season) in the analysis of trap captures seem to reduce the effect of the activity component in trapping systems (Baars 1979, Colunga-Garcia 1996). Estimates were conducted for individual species as well as for the complex of coccinellids (i.e., by summing all individuals regardless of species).

Species Richness. This was determined as the average number of species captured per trap.

Species Dominance (d). This was estimated using the Berger–Parker equation d = $N_{\max}/N_{\text{tot}}$, in which $N_{\max}$ is the number of insects of the most abundant species and N_{tot} is the number of insects for all the species measured in the sample (Magurran 1988). This index measures the proportional abundance of the most abundant species, is independent of the number of species, and has low sensitivity to sample size (Southwood 1978). When combined, the number of species and the Berger–Parker index can provide more information on species diversity than the Shannon–Wiener or the Simpson indices alone (Magurran 1988). Relative abundance, species richness, and species dominance were estimated for every sampling week at each of the 3 sites. Data were normalized before statistical analysis was done using a $\sqrt{x + 0.001}$ transformation. Analysis of variance (ANOVA) and the Tukey honestly significant difference (HSD) test were used to test for statistically significant differences among sites (SPSS 1993). The ANOVA was conducted using the 37 weekly estimations as replicates because spatial replication was not feasible at the scale of this study (Hargrove and Pickering 1992).

Kendall Rank Correlation. Kendall's coefficient (τ) was used as a measure of similarity between species ranking of different sites (Southwood 1978). Estimation of τ was based on the mean trap captures per site using the Kendall rank correlation test (Kendall 1955, SPSS 1993). For this analysis, rare species (<4 adults captured per site) were eliminated (Bullock 1971).

Principal Component Analysis (PCA). This is a multivariate technique that facilitates the reduction in dimensions of the original variables to produce a small number of variables (components) ordered by the amount of variance they explain (James and McCulloch 1985). Because PCA requires the existence of linear combination of the original variable, data were log-transformed ($\sqrt{x + 0.001}$) before analysis. Before using PCA, the data were arranged on a matrix in which sites were the headings of the columns and species were the headings for the rows (SPSS 1993). Each intersection row (r)-column (c) had a value that represented the mean trap captures of the species r in the site c. Interpretation of components is conducted by constructing plots using component values as graphical coordinates (Randerson 1993). For each PCA, 2 plots were produced. The 1st plot used the components for coccinellid species (also known as eigenvalues), and the 2nd plot used the components for sites (also known as scores). Visual interpretation of components is greatly reinforced with the use of both plots together (Randerson 1993).

Species Assemblage and Landscape Characteristics. Each site was characterized by estimating habitat dominance and relative patchiness using the primary habitat type at each sampling station. To estimate the habitat dominance, all the habitats (cultivated and noncultivated) within a site were included. Additionally, crop and noncrop dominance were estimated by considering only crop and noncrop habitats, respectively. Dominance was estimated using the Berger–Parker equation as described previously. Relative patchiness (P) was estimated using the equation: $P = (\Sigma D_i/N) \times 100$ (Turner 1989), where D_i is the dissimilarity value for the ith boundary between adjacent cells for a same habitat and 1 for a different habitat) and N is the number of boundaries between adjacent cells. Each 100-m^2 quadrat, in whose centroid a sampling station was placed, was considered as one cell (Fig. 1).

The degree of correlation between site scores produced from the PCA and landscape indices (habitat dominance and relative patchiness) was estimated using the Pearson product–moment correlation coefficient (SPSS 1993).

A separate analysis was conducted to determine if alfalfa, the only crop habitat that was present in all 3 sites, could reflect the species assemblage patterns observed in the entire site. A subset of data from each site was selected which consisted of coccinellid captures from 6 continuous sampling stations located in alfalfa. Analysis of species assemblage was conducted on these alfalfa data subsets by estimating relative abundance, species richness, species dominance, and the Kendall coefficient. To check for differences in coccinellid relative abundance in alfalfa caused by differences in food availability, the relative abundance of aphids was estimated using sweep sampling. Ten sweeps per sampling station were conducted in alfalfa the same day that sticky trap counting was made. Insects collected were put in paper bags, frozen, and all aphids were counted. Data were normalized using a $\sqrt{x + 0.001}$ transformation. ANOVA and the Tukey HSD test were used to test for statistically significant differences among sites (SPSS 1993).

Results

Species Assemblages. *Species Richness.* Overall, 13 species of coccinellids were sampled in this study—*Coccinella septempunctata* (L.), *Cycloneda munda* (Say), *Coleomegilla maculata lengi* Timberlake, *Adalia bipunctata* (L.), *Brachiacantha ursina* (F.), *Chilocorus stigma* (Say), *Hippodamia parenthesis* (Say), *Hippodamia convergens* Guérin-Méneville, *Coccinella trifasciata perplexa* Mulsant, *Hippodamia tredecimpunctata tibialis* (Say), *Hyperaspis undulata* (Say), *Anatis labiculata* (Say), and *Coccinella novemnotata* Herbst. The highest richness index ($n = 37$) was observed in site 3 (4.8 ± 0.3) (mean ± SE) ($P = 0.002$), and no significant difference was detected between site 1 (3.2 ± 0.3) and site 2 (3.3 ± 0.3) ($P = 1.00$).

Relative Abundance. Significant differences among sites were detected for 4 species. *C. m. lengi* was more abundant in site 2 ($P \leq 0.003$), whereas *C. munda*, *C. stigma*, and *B. ursina* were more abundant in site 3 ($P \leq 0.003$) (Fig. 2). The rest of the coccinellid species, including *C. septempunctata*, the dominant coccinellid in the landscape, showed no significant preference for any site ($P > 0.15$). Mean trap captures obtained in

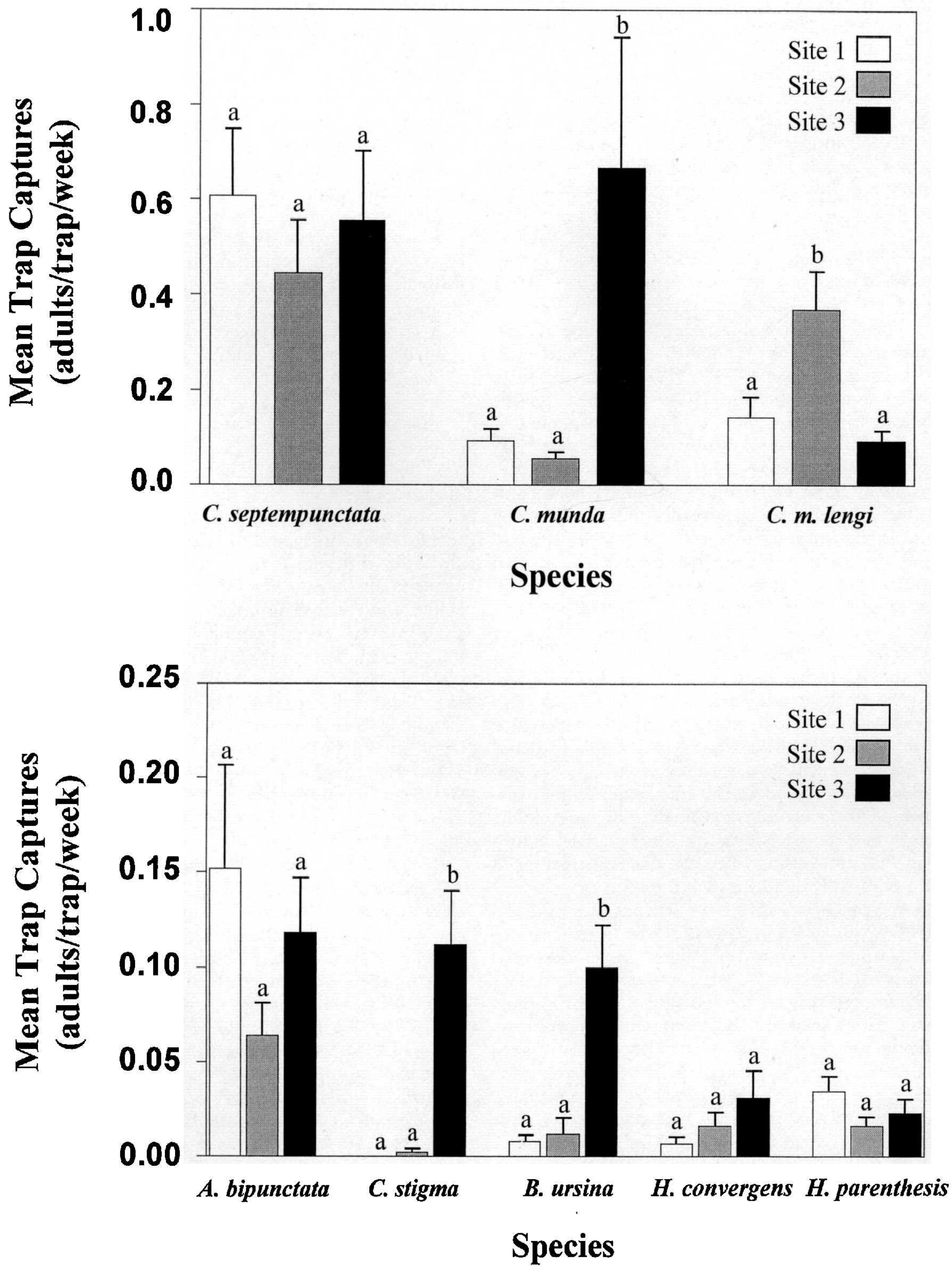

Fig. 2. Mean ± SE trap captures of 8 species of coccinellids sampled using yellow sticky traps within each of 3 sites having different habitat configuration (500 by 500 m) at the Kellogg Biological Station, Hickory Corners, MI, during 1989–1990. Primary habitats in each site were site 1, field succession and alfalfa; site 2, field succession, alfalfa, and corn; site 3, field succession, deciduous vegetation, alfalfa, and wheat.

Table 1. Mean ± SE trap captures per week of 13 species of coccinellids sampled during 37 wk using yellow sticky traps within site 1; Kellogg Biological Station, Hickory Corners, MI; 1989–1990

Species name	Alfalfa (n = 10)	Field succession (n = 15)
C. septempunctata	0.865 ± 0.103	0.483 ± 0.076
C. munda	0.009 ± 0.005	0.140 ± 0.072
C. m. lengi	0.078 ± 0.015	0.185 ± 0.049
A. bipunctata	0.124 ± 0.022	0.173 ± 0.048
B. ursina	0	0.013 ± 0.005
H. convergens	0	0.011 ± 0.004
H. parenthesis	0.031 ± 0.007	0.038 ± 0.013
H. undulata	0.003 ± 0.003	0.002 ± 0.002
C. t. perplexa	0	0.002 ± 0.002
H. t. tibialis	0.003 ± 0.003	0
A. labiculata	0	0
C. novemnotata	0	0
C. stigma	0	0

individual habitats within a site are shown in Tables 1–3. The relative abundance (n = 37) of the coccinellid complex was: site 1 = 1.1 ± 0.2, site 2 = 1.0 ± 0.1, and site 3 = 1.7 ± 0.3. Site 2 and 3 were significantly different (P = 0.043).

Species Dominance. Similar species dominance indices (n = 37) were observed among sites: site 1 = 0.66 ± 0.04, site 2 = 0.64 ± 0.04, and site 3 = 0.52 ± 0.4 (P > 0.07).

Concordance. Kendall's coefficient of concordance showed that site 1 and site 2 had a significant degree of similarity (τ = 0.79, P = 0.006), whereas site 3 was significantly different from site 1 (τ = 0.29, P = 0.322) and site 2 (τ = 0.21, P = 0.458).

Principal Component Analysis. Graphical assessment of the principal components of species and the site scores showed that the 1st component, which accounted for 90% of the variance, was related to intrinsic differences among coccinellid species. In this 1st component, the outcome of the analysis arranged the species from the most abundant, *C. septempunctata* on the positive side of the axis, to the least abundant, *C. novemnotata* and *A. labiculata* on the negative side of the axis (Fig. 3). The lack of habitat effect in this component was evident from the fact that the 3 sites retained the same position along the 1st score axis. Therefore, the 1st component described the assemblage of coccinellid species at a scale that included all sites. The 2nd principal component, which accounted for 9% of the variance, was a result of site differences. *C. munda*, *B. ursina*, and *C. stigma*, which were more abundant in site 3, were positioned on the positive side of the axis, whereas species such as *C. m. lengi*, which were more abundant in sites 1 or 2, were positioned on the negative side of the 2nd component axis as a result of the analysis. The PCA scores grouped site 1 and site 2 separately from site 3, which confirmed our observations that more noticeable effects on species assemblages of coccinellids occurred in site 3.

Species Assemblage and Landscape Characteristics. The distribution of primary habitats in the 3 sites as described by the habitat present at each sampling station is shown in Fig. 1. Site 1 was considered to have the most simple structure, whereas site 3 was considered the most complex, given its high relative patchiness and low noncrop dominance (Table 4).

The 2nd PCA score, which grouped site 1 and site 2 separately from site 3, suggested that some feature of site 3 had a different influence on coccinellid species assemblages (Fig. 3). The correlation between the 2nd site score and the landscape indices (Table 4) showed the possible effect of noncrop dominance (r = −0.99, P = 0.0198) and relative patchiness (r = 0.99, P = 0.1305) (Fig. 4), which were in turn the 2 features of the landscape in which site 1 and site 2 were more similar to each other and different from site 3.

Landscape Influence in Alfalfa Habitat. In alfalfa, *C. munda* and *B. ursina* were significantly more abundant in site 3 ($P \leq 0.013$). Also in this habitat, significant differences were observed between sites 2 and 3 for *C. septempunctata* (P = 0.037) and between sites 1 and 3 for *H. convergens* (P = 0.04). The relative abundance (n = 37) of the entire coccinellid complex was significantly higher in site 3 (2.3 ± 0.4) ($P \leq 0.009$) and no significant

Table 2. Mean ± SE trap captures per week of 13 species of coccinellids sampled during 37 wk using yellow sticky traps within site 2; Kellogg Biological Station, Hickory Corners, MI; 1989–1990

Species name	Alfalfa (n = 9)	Field succession (n = 10)	Corn (n = 4)
C. septempunctata	0.704 ± 0.189	0.398 ± 0.092	0.140 ± 0.036
C. munda	0.046 ± 0.014	0.021 ± 0.008	0.169 ± 0.030
C. m. lengi	0.327 ± 0.082	0.099 ± 0.017	1.352 ± 0.170
A. bipunctata	0.096 ± 0.051	0.040 ± 0.012	0.026 ± 0.017
B. ursina	0.007 ± 0.004	0.003 ± 0.003	0.046 ± 0.035
H. convergens	0.031 ± 0.014	0.012 ± 0.007	0
H. parenthesis	0.017 ± 0.007	0.021 ± 0.010	0.009 ± 0.009
H. undulata	0.003 ± 0.003	0	0.009 ± 0.009
C. t. perplexa	0.003 ± 0.003	0	0
H. t. tibialis	0	0.003 ± 0.003	0
A. labiculata	0	0	0
C. novemnotata	0.003	0	0
C. stigma	0.003	0	0

Table 3. Mean ± SE trap captures per week of 13 species of coccinellids sampled during 37 wk using yellow sticky traps within site 3; Kellogg Biological Station, Hickory Corners, MI; 1989–1990

Species name	Alfalfa (n = 6)	Field succession (n = 10)	Wheat (n = 1)	Deciduous (n = 7)
C. septempunctata	1.303 ± 0.180	0.512 ± 0.175	0.278	0.063 ± 0.031
C. munda	0.331 ± 0.291	0.456 ± 0.166	1.472	1.120 ± 0.444
C. m. lengi	0.227 ± 0.033	0.046 ± 0.021	0.222	0.043 ± 0.008
A. bipunctata	0.139 ± 0.067	0.066 ± 0.028	0.361	0.131 ± 0.060
B. ursina	0.173 ± 0.108	0.054 ± 0.011	0.056	0.103 ± 0.042
H. convergens	0.093 ± 0.042	0.019 ± 0.008	0.028	0
H. parenthesis	0.034 ± 0.014	0.027 ± 0.011	0.056	0.004 ± 0.004
H. undulata	0	0.003 ± 0.003	0	0.008 ± 0.008
C. t. perplexa	0	0.003 ± 0.003	0.028	0.004 ± 0.004
H. t. tibialis	0.005 ± 0.005	0	0	0
A. labiculata	0	0	0	0.004 ± 0.004
C. novemnotata	0	0	0	0
C. stigma	0.010 ± 0.006	0.093 ± 0.034	0.083	0.227 ± 0.057

differences were observed between site 1 (1.1 ± 0.2) and site 2 (1.3 ± 0.2) (P = 0.89). Species richness (n = 37) also was highest in site 3 (2.8 ± 0.2) ($P \leq 0.01$), and no difference was observed between site 1 (1.4 ± 0.1) and site 2 (1.8 ± 0.2) (P = 0.7). Similar species dominance was observed among alfalfa habitats in the 3 sites: site 1 (0.73 ± 0.06), site 2 (0.62 ± 0.06), and site 3 (0.56 ± 0.4) ($P > 0.4$).

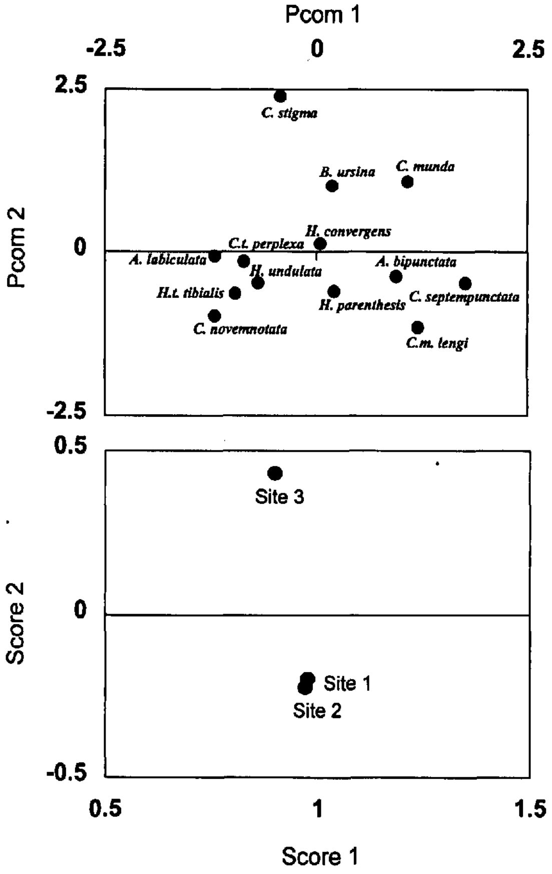

Fig. 3. Site scores and principal components based on the analysis of 13 species of coccinellids captured at 3 sites at the Kellogg Biological Station, Hickory Corners, MI, during 1989–1990. Primary habitats in each site were site 1, field succession and alfalfa; site 2, field succession, alfalfa, and corn; site 3, field succession, deciduous vegetation, alfalfa, and wheat.

The Kendall coefficient showed that species concordance in alfalfa from site 1 and site 2 was high (τ = 0.72, P = 0.016), whereas there was no concordance between site 3 and site 1 (τ = 0.34, P = 0.252) and between site 3 and site 2 (τ = 0.50, P = 0.083). Finally, no difference was observed on the relative abundance of aphids (mean per sweep: site 1 = 3.60 ± 0.8, site 2 = 2.1 ± 0.6, and site 3 = 2.9 ± 0.9 ($P \geq 0.13$).

Discussion

In this study, a gradient of landscape complexity was selected, in which site 1 (with 1 crop and 1 noncrop habitat) was the simplest landscape and site 3 (with 2 crop and 2 noncrop habitats) was the most complex. Site 2 (with 2 crop and one noncrop habitat) was intermediate. Therefore, it was expected that this gradient would affect the species assemblage of coccinellids. Results showed that the habitat structure of site 3 was different enough from the other 2 sites to produce an effect on the species assemblage of coccinellids. No significant differences, however, were detected between sites 1 and 2 (other than a higher relative abundance of *C. m. lengi* in site 2). Therefore, the possibility that crop dominance had an effect on the community structure of coccinellids was discarded at this scale

Table 4. Landscape characterization of 3 sites using the Berger–Parker dominance index and the relative patchiness index based on primary habitat types

Index	Site 1	Site 2	Site 3
Habitat dominance	0.6	0.4	0.4
Crop dominance	1.0	0.7	0.9
Noncrop dominance	1.0	1.0	0.6
Relative patchiness	26	19	57

Primary habitats: site 1, field succession and alfalfa; site 2, field succession, alfalfa, and corn; site 3, field succession, deciduous forest, alfalfa, and wheat.

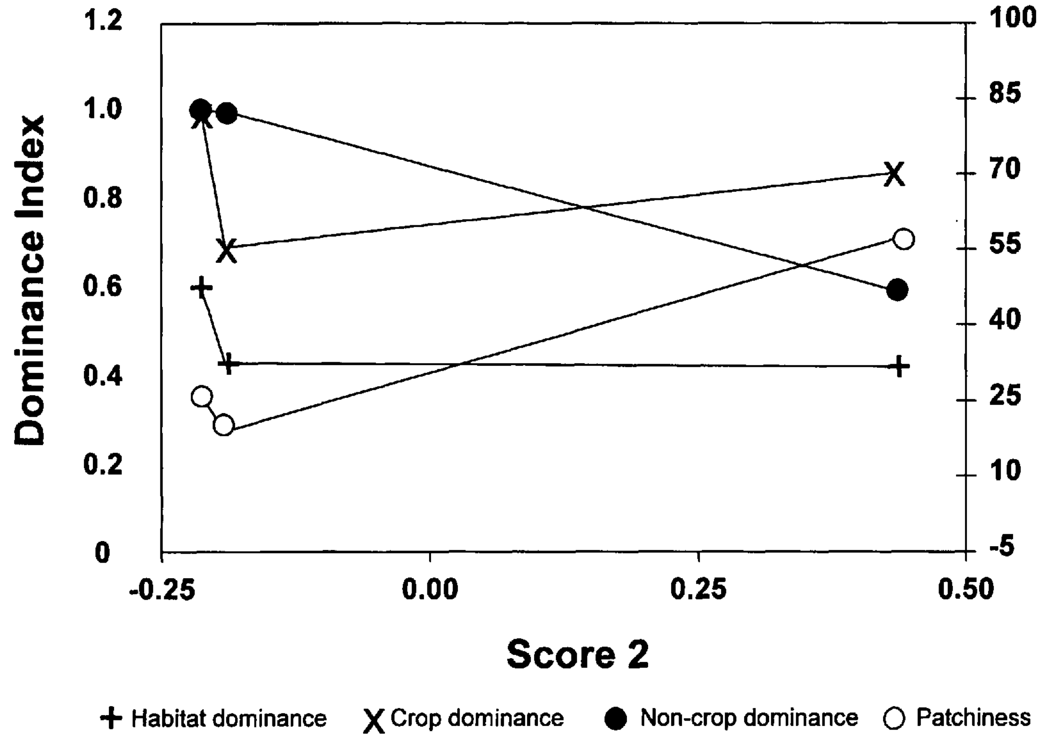

Fig. 4. Association between landscape indices of 3 sites and 2nd score of same sites after a principal component analysis of 10 species of coccinellids captured at 3 sites at the Kellogg Biological Station, Hickory Corners, MI, during 1989–1990. Primary habitats in each site were site 1, field succession and alfalfa; site 2, field succession, alfalfa, and corn; and site 3, field succession, deciduous vegetation, alfalfa, and wheat.

of analysis. From the set of landscape indices used to characterize the 3 sites, only the noncrop dominance and the patchiness indices were most likely to influence coccinellid species assemblages. The noncrop dominance index, however, used to characterize uncultivated habitats was a measure that did not take into account habitat quality. All 3 sites had field succession, but only site 3 had a mature deciduous forest. In this study, it was more important that site 3 had a deciduous habitat than having 2 uncultivated habitats. On the other hand, the results of this study did not rule out the importance of field succession as an alternate habitat for predators in the landscape. Because such habitat was present in all 3 sites, its effect on the species assemblages of coccinellids could have been equally distributed and therefore not noticeable. The presence or absence of deciduous habitats seemed to explain the major differences observed in this study. However, because relative patchiness also was an important landscape characteristic distinguishing site 3 from the other 2 sites, it was important to consider the possibility of an effect by this factor. Patchiness at small scales can affect the searching capacity of coccinellids (Kareiva 1987). However, the effect of large-scale patchiness on population dynamics of natural enemies is not known. With predators such as coccinellids, which have high capabilities for dispersal and wide preference for several habitats, large-scale patchiness may force them to disperse among habitats (Ives 1981). An increase in the pattern of activity in a patchy landscape could have explained why, overall, more insects were captured in site 3. However, *C. septempunctata*, the dominant species in the landscape, had similar abundance in all sites, indicating that patchiness did not significantly affect its pattern of activity.

In the analysis conducted on coccinellids in the alfalfa habitat, the highest species richness observed in site 3 showed the potential effect of habitat configuration on the assemblage of species of predators. Species such as *C. munda* and *B. ursina*, for example, showed high relative abundance in all of site 3. Because no statistically significant differences were found between aphid populations in the 3 sites, the differences observed in the total relative abundance of coccinellids, as well as the relative abundance of species such as *C. septempunctata* and *H. convergens* in alfalfa, could be the result of landscape–insect factors that were not addressed in this study.

Increasing habitat diversity has been suggested as a way to enhance natural control of pests in agroecosystems by providing natural enemies with alternative sources of food, shelter, and other resources (Altieri 1994). In this study we observed an increase in the number of species of coccinellids present in field crops in landscapes where local habitat diversity was increased by the presence of uncultivated habitats. We did not examine if coccinellid abundance in sticky traps was correlated with measures in the crop canopy itself. However, in another study we found that trap captures of coccinellids in wheat at the height used in this study are highly correlated with traps placed at the canopy of the crop (Colunga-Garcia 1996). In the same study, it was found that when samples are pooled over an entire season, sticky trap and sweep net captures of coccinellids also are highly correlated. In field crops, there are some species such as *A. bipunctata* that are captured in sticky traps but rarely by sweep net sampling (Kieckhefer et al. 1992). This suggests that some coccinellid species, which are typical of deciduous habitats, may reside only sporadically in the crops. In this case, an increase in the number of coccinellid species present in a crop may or may not translate to a better regulation of economic pests. In this study, the lack of pest outbreaks in field crops did not allow us to obtain evidence for any of those 2 possibilities.

Considering the entire complex of natural enemies, an increase in the presence of species in a crop may be beneficial for the natural regulation of pests. However, further studies will be needed in which landscapes are manipulated to produce deciduous areas to enhance the presence of predators in habitats where pest outbreaks often occur.

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