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Effects of an invading coccinellid on native coccinellids in an agricultural landscape

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Abstract Seven native coccinellid species inhabited alfalfa, corn, and small grain fields in eastern South Dakota prior to invasion and establishment of *Coccinella septempunctata* L. Six species occurred in all crops, however, *Adalia bipunctata* (L.) occurred only in corn. The structure of native coccinellid communities differed significantly for years prior to compared with years after establishment of *C. septempunctata* in fields of the three agricultural crops. Differences in community structure were accounted for mainly by reduced abundance of two species, *C. transversoguttata richardsoni* Brown and *Adalia bipunctata* (L.). Annual abundance of *C. transversoguttata richardsoni* averaged 20–32 times lower during post-invasion years than in years prior to invasion, depending on crop; while annual abundance of *A. bipunctata* averaged 20 times lower in corn after invasion. Addition of *C. septempunctata* to the community did not result in a significant increase in total abundance of coccinellids in the crops. Coccinellid abundance in agricultural crops may be limited by the total abundance of prey or by the availability of other requisites in the landscape as a whole. Therefore, introduction of a new species, while resulting in reductions in native species populations, may not increase total coccinellid abundance, and may therefore have no net effect on biological control of aphid pests.

Key words Coccinellidae · Aphididae · Biological control · Competition

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Introduction

Classical biological control involves the importation and establishment of exotic natural enemies for the express purpose of reducing pest populations below levels at which they cause economic injury to crops. Classical biological control has been remarkably effective for this purpose, and numerous successful projects are documented where established natural enemies have reduced or eliminated the need for insecticides to control pest insects (Caltagirone 1981). Successful biological control projects have usually been conducted against exotic pests, control of which is attributed to the fact that accidentally introduced species became pests in a new region because they were released from control by natural enemies. Control is regained by the establishment of natural enemies in the new region.

A desirable feature of classical biological control is that it involves no environmental contamination of the type associated with some chemical control methods. However, the introduction of a new organism into the environment is in itself a form of contamination, and can be significant from the perspective of species conservation. Negative impacts of introduced exotics include competitive suppression or displacement of native natural enemies and suppression or extinction of non-target prey species, some of which may be beneficial. The potential for eliminating native species by establishment of exotics is more than speculative. Howarth (1991) reviews several examples where populations of native species were severely reduced or eliminated, apparently by introduced exotic natural enemies.

In ephemeral agroecosystems, such as most field crop ecosystems, predaceous insects assume an important role in biological control of insect pests (Ehler and Miller 1978; Luff 1983). Characteristics of predatory insects identified as important biological control agents in ephemeral cropping systems include ability to rapidly colonize new habitats, ability to persist in the ecosystem in the absence of the target pest species, and opportunistic feeding habits (Ehler and Miller 1978; Luff 1983).

The last two factors are most often associated with polyphagous predators. Polyphagous species exhibit potential for controlling insect pests of ephemeral crops, yet these same species may pose a greater threat to native species than oligophagous or monophagous species (Samways 1988). Thus, there is a potential conflict between the goals of biological control and species conservation.

The seven-spotted lady beetle, *Coccinella septempunctata* L. (referred to hereafter as C7) is a dominant coccinellid in agricultural and non-agricultural ecosystems in the Palearctic region (Hodek 1973). C7 feeds on a wide variety of aphid species occurring in numerous agricultural and non-agricultural ecosystems (Hodek 1973; Honek 1982a, b, 1983, 1985), and sometimes feeds on other insects (Hodek 1973). C7 can be considered both polyphagous and a habitat generalist. Because of its large size and voracious appetite, C7 was considered a promising candidate for biological control of a variety of aphid pests of crops. Between 1957 and 1990 C7 was imported and released at various locations in the United States. The coccinellid was first established in 1973 and underwent a rapid range expansion during the 1980s, and by 1987 it had established populations throughout most of continental USA (Schaefer et al. 1987).

Because of its broad habitat range and voracity there has been concern that C7 may competitively displace some native aphidophagous coccinellids (Staines et al. 1990; Howarth 1991). R.D. Gordon (unpublished data) observed unusually low abundances of native Coccinellini in field surveys in areas where C7 had recently established thriving populations. However, surveys conducted for only one or a few years can yield misleading information regarding the structure of coccinellid species assemblages because native coccinellid populations typically undergo large and unpredictable fluctuations in abundance from year to year (Elliott and Kieckhefer 1990a, b; Kieckhefer and Elliott 1990), thus reducing the value of studies conducted over short time horizons. Long-term studies conducted at the same location are often essential to reliably delineate trends or patterns in ecological processes that exhibit high temporal variability (Franklin 1989). Long-term monitoring of native coccinellid populations prior to and after establishment may provide the information needed to determine if invasion by C7 has had an adverse effect on native coccinellid populations.

This study was conducted to determine whether the structure of coccinellid species assemblages in agricultural crops (alfalfa, corn, and small grains) in eastern South Dakota was altered by invasion and establishment of C7 in the region in 1987. Coccinellid assemblages in these crops were intensively monitored for 13 years prior to, and 5 years after, the establishment of C7 in the region. Resulting data were used to compare coccinellid species abundances and community structure prior to, and after, establishment.

Materials and methods

Adult coccinellids were sampled in a single commercial field of alfalfa, corn, and small grain at each of three study sites in eastern South Dakota for 13 years (1973–1985) prior to the invasion of eastern South Dakota by C7 in 1987, and 5 years (1988–1992) after invasion and establishment of C7. The study sites were designated as Moody Co., Hamlin Co., and Deuel Co., referring to the county in which the particular site was located. The procedures used to sample coccinellids are described in detail elsewhere (Elliott and Kieckhefer 1990a, b; Kieckhefer and Elliott 1990); only a brief account of sampling procedures is presented here. Sampling in alfalfa and small grains was accomplished by taking six 50-sweep samples (total of 300 sweeps) in each field with a 38-cm diameter sweepnet at approximately weekly intervals throughout the portion of the growing season of each crop during which coccinellids were present in it. Sampling in corn was accomplished by making four 15-min visual searches of corn plants within a field at approximately weekly intervals. Average annual abundance and occurrence (presence/absence) of each species in a particular crop at a location were calculated from combined weekly samples. Average annual abundances were subsequently used to investigate the effect of invasion by C7 on native coccinellid assemblages.

Methods described by Clarke (1993) were used to determine whether invasion and establishment of C7 was associated with a change in community structure in each crop, and included: (1) calculation of Bray-Curtis dissimilarity coefficients (Bray and Curtis 1957) from native species occurrence data (occurrence data for C7 were not included) for all pairwise samples from a crop at a location for the 13 years prior, to and 5 years after invasion; (2) identification of the species principally responsible for observed sample dissimilarities; and (3) non-parametric statistical tests for differences in community structure before versus after C7 invasion based on rank dissimilarity indices for within-group and between-group comparisons. The basis of the test is that if differences in community structure exist among groups, within-group rank dissimilarities would usually be smaller than between-group rank dissimilarities. Analyses were conducted using species occurrence data to emphasize the contributions of uncommon species to community patterns. The null hypothesis of no difference in structure between pre- and post-invasion communities was tested using the following statistic (Clarke 1993):

$$R=(r_b-r_w)/(M/2) \quad (1)$$

where r_w is the average of all rank dissimilarities among samples within groups (either prior to or after invasion), r_b is the average of all rank dissimilarities among samples between groups (prior to invasion compared with after invasion), and $M=n(n-1)/2$, where n equals the total number of samples. An empirical probability distribution of R under the null hypothesis of no difference in community structure among groups was constructed for each test by generating 2500 values of R, each based on rank dissimilarities calculated from groups created by a random permutation of all samples.

The Mann-Whitney U test (SAS Institute 1988, pp 714–726) was used to compare pre- and post-invasion abundances of each native species in a crop. Prior to conducting pairwise statistical tests, Durbin-Watson statistics (Durbin and Watson 1971) were calculated to test for serial correlation in each species' annual abundance time series for each crop. Dependency among years in the average abundance of a species would invalidate the use of the Mann-Whitney U statistic for hypothesis testing due to lack of sample independence.

Results

An average of 29.4 and 18.3 300-sweep samples were taken from alfalfa and small grain fields respectively, each year; and an average of 17.1 1-h searches were

made in corn each year (Table 1). Thus, the abundance of a species in a year was based on an average of 8817 sweeps in alfalfa and 5500 sweeps in small grains, and a total of 1027 min of searching in corn. The number of samples taken from a crop during a year varied (Table 1) due to factors such as the length of the growing season, which varied among years, drought, which in some years caused premature senescence or death of crop plants, and extended periods to rainfall, which occasionally curtailed sampling.

Seven native aphidophagous coccinellid species were captured in alfalfa, corn and small grain fields in eastern South Dakota. *Hippodamia convergens* Guerin-Meneville was the most abundant coccinellid in all crops; a total of 3890, 8854, and 2662 *H. convergens* were collected in alfalfa, corn and small grains, respectively, during the 18-year study (Table 2). *H. tredecimpunctata tibialis* (Say), *H. parenthesis* (Say), and *Coleomegilla maculata lengi* Timberlake were also relatively abundant (Table 2), however *H. parenthesis* was infrequently captured in corn. *Coccinella transversoguttata richardsoni* Brown, *Cycloneda munda* (Say), and *Adalia bipunctata* (L.) were uncommon, with fewer than 267 individuals of any of the three species captured in any crop during the 18 years. All species except *A. bipunctata* were captured in all three crops but *A. bipunctata* occurred only in corn. Catch of all species varied markedly among years. For example, catch of *H. convergens* in alfalfa varied by more than an order of magnitude from the highest (512 individuals) to lowest (23 individuals) total annual catch recorded (Table 2). Catch of other species was similarly variable among years.

Species abundances were generally correlated among sites within the same year (Table 3). The presence of such correlation indicates that populations at the three study sites were not independent. Thus, it would be inappropriate to consider sites as independent replicates from the standpoint of assessing the impact of C7 on native coccinellid communities. Consequently, data within years and crops from the three study sites were combined to obtain a single estimate of average abundance for each species for each year.

Annual abundances of the seven native species and C7 in alfalfa, corn, and small grain fields averaged across study sites are illustrated in Figs. 1–3. All species underwent large changes in abundance from one year to the next, both prior to, and after invasion by C7. Some species exhibited generally lower abundances after invasion. For example, abundance of *H. tredecimpunctata tibialis* appeared, on average, to have decreased in all crops from 1988 through 1992 when compared with

Table 1 Mean number (range) of 300-sweep samples taken per year in alfalfa and small grains, or 1-h visual searches per year in corn, and mean number of sweeps or minutes searching per year during 18 years (1973–1985 and 1988–1992)

Crop	Mean no. samples/year (range)	Mean no. sweeps or min/year
Alfalfa	29.4 (24–47)	8816.7
Corn	17.1 (11–24)	1026.7
Small grains	18.3 (13–24)	5500.0

Table 2 Total number of adult coccinellids captured in sweep-net samples from alfalfa and small grains and visual searches in corn during 18 years (1973–1985 and 1988–1992). *Coccinella septempunctata* was present in samples only during 1988–1992. Numbers caught in the year with minimum and maximum total catch in each crop are listed in parentheses

Species	Alfalfa	Corn	Small grains
Hippodamia convergens	3890 (23–512)	8854 (41–1426)	2662 (11–462)
H. tredecimpunctata tibialis	1465 (0–245)	5227 (8–684)	1627 (1–384)
H. parenthesis	1316 (4–225)	138 (0–75)	581 (0–142)
Coleomegilla maculata lengi	682 (0–153)	6046 (20–1177)	448 (1–134)
Cycloneda munda	46 (0–10)	128 (0–51)	65 (0–28)
Coccinella transversoguttata richardsoni	99 (0–34)	266 (0–62)	74 (0–31)
Adalia bipunctata	0	41 (0–9)	0
C. septempunctata	456 (9–150)	453 (4–216)	378 (6–202)

Table 3 Correlation coefficients among average annual abundances of native coccinellid species within years at three sites during 18 years (1973–1985 and 1988–1992)

Species	Alfalfa			Corn			Small grains		
	Moody/ Hamlin	Moody/ Deuel	Hamlin/ Deuel	Moody/ Hamlin	Moody/ Deuel	Hamlin/ Deuel	Moody/ Hamlin	Moody/ Deuel	Hamlin/ Deuel
Hippodamia convergens	0.39	0.51*	0.49*	0.80*	0.71*	0.71*	0.74*	0.39	0.63*
H. tredecimpunctata tibialis	0.28	0.38	0.69*	0.21	0.33	0.63*	0.47*	0.31	0.44*
H. parenthesis	0.10	0.62*	0.28	0.08	0.01	0.28	0.46*	0.25	0.54*
Coleomegilla maculata lengi	0.58*	0.76*	0.79*	0.76*	0.71*	0.73*	0.73*	0.81*	0.72*
Cycloneda munda	0.69*	0.33	0.73*	0.89*	0.75*	0.81*	0.78*	0.51*	–0.09
Coccinella transversoguttata richardsoni	0.81*	0.91*	0.85*	0.41	0.74*	0.26	0.22	0.53*	–0.08
Adalia binpunctata	–	–	–	0.23	0.52*	0.72*	–	–	–

* Significantly different from zero (α=0.05)

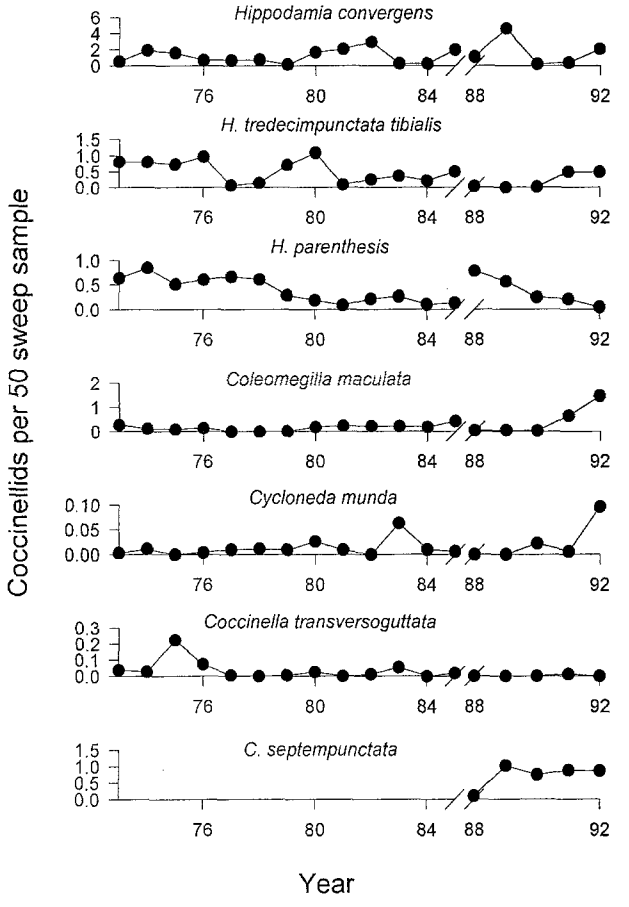

Fig. 1 Mean annual coccinellid abundance in alfalfa fields in eastern South Dakota from 1973–1992. Note differences in scale of *vertical axes*

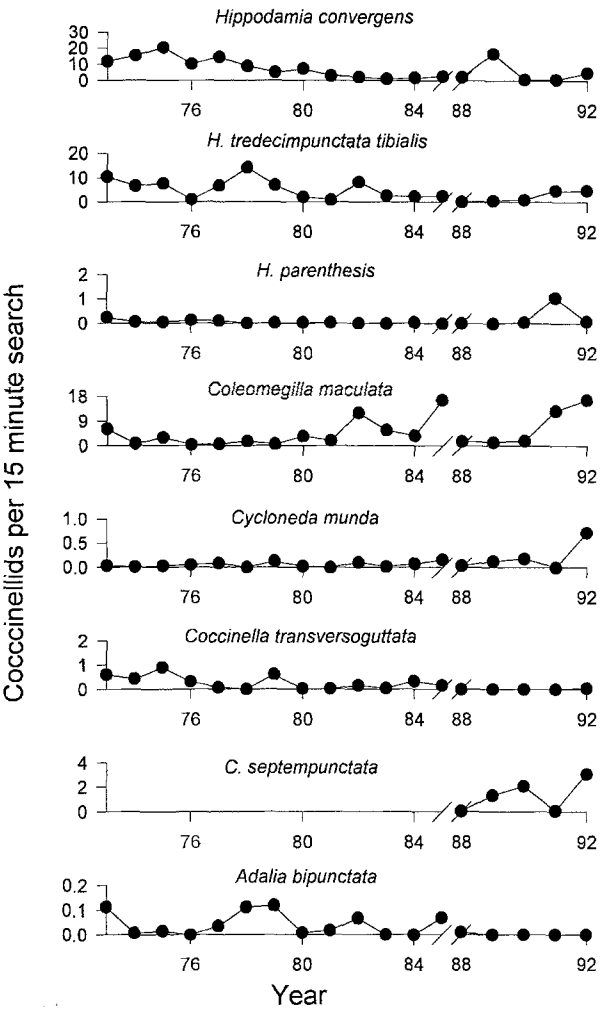

Fig. 2 Mean annual coccinellid abundance in corn fields in eastern South Dakota from 1973–1992. Note differences in scale of *vertical axes*

years prior to invasion. Two species, *C. transversoguttata richardsoni* and *A. bipunctata*, decreased markedly in abundance after invasion. Annual abundances of *C. transversoguttata richardsoni* decreased on average by about an order of magnitude in all crops after invasion (Figs. 1–3). Average annual abundance of *A. bipunctata* in corn decreased a similar amount after invasion (Fig. 2). Abundance of *C. maculata lengi* increased from 1988 through 1992 to approximately twice that of pre-invasion years. While *C. maculata lengi* increased in abundance in all crops, the increase in abundance, in relative terms, appeared considerably smaller than decreases in abundance of *C. transversoguttata richardsoni* and *A. bipunctata*.

Patterns in species abundances suggest that a change in community structure occurred coincident with C7 invasion. However, inspection of species abundance time series suggests that prior to invasion several species underwent periods during which abundance was unusually high or low that extended for several years. In that case, a change in community structure that occurred at about the time C7 invaded could simply be a realization of an ongoing process rather than the result of interaction with C7. To guard against that possibility, we used Clarke's (1993) method for detecting community change on subsets of the data, in addition to analyzing the total data set.

First, data from three 5-year periods were extracted from the total of 18 years' data. These periods were, 1974–1978, 1981–1985, and 1988–1992. *R*-statistics were calculated for two groupings of these data for each crop to test for change in community structure. In the first comparison, data from 1974–1978 were compared with data from 1981–1985. In the second comparison, data from 1981–1985 were compared with data from 1988–1992. Partitioning the data in this way permitted us to compare time intervals of identical length (5 years) separated by the same interval (2 years), except that in the second comparison C7 was present as a factor. Species occurrence rather than abundance data were used in calculating Bray-Curtis dissimilarities in order to emphasize fluctuations in populations of uncommon species because visual inspection of the data indicated that abundances of such species changed most after invasion.

R-statistics for all three crops for the 1981–1985 with 1988–1992 comparison differed significantly from zero

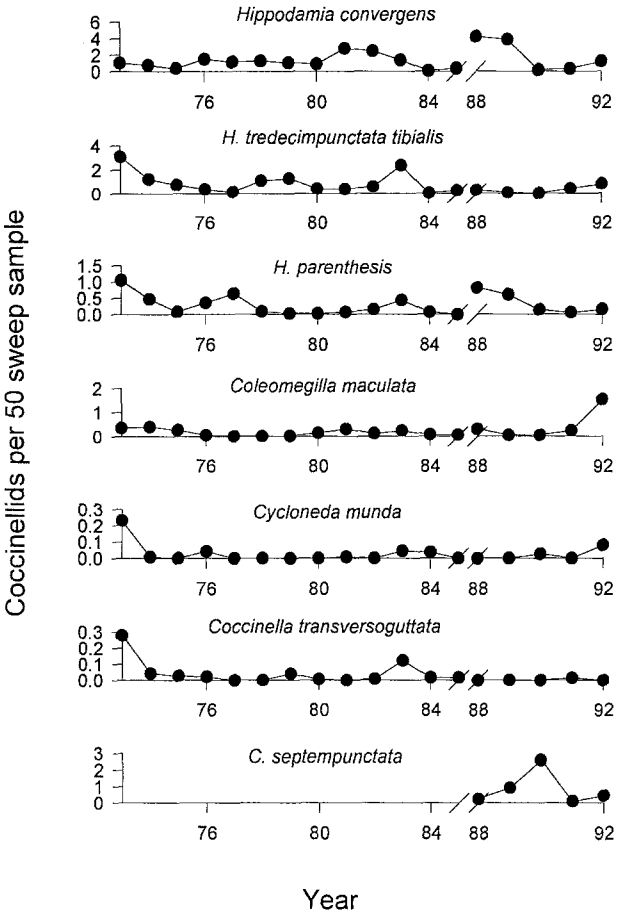

Fig. 3 Mean annual coccinellid abundance in small grain fields in eastern South Dakota from 1973–1992. Note differences in scale of *vertical axes*

Table 4 Average (SE) contribution of coccinellid species to Bray-Curtis dissimilarity in three agricultural crop during two groups of five consecutive years extracted from the total of 18 years' data. *A bipunctata* was present only in corn

Statistic/Crop	Species 1974–78 vs 1981–85	Comparison 1981–85 vs 1988–92
R-statistics		
Alfalfa	–0.058	0.224*
Corn	–0.164	0.310*
Small grains	–0.030	0.376*
Bray-Curtis Dissimilarity		
Alfalfa		
Hippodamia convergens	0	0
H. tredecimpunctata tibialis	0	2.28 (0.93)
H. parenthesis	0	0
Coleomegilla maculata lengi	2.13 (0.87)	0
Cycloneda munda	3.06 (0.91)	6.18 (1.04)
Coccinella transversoguttata richardsoni	4.23 (0.98)	6.69 (0.95)
Total dissimilarity	9.42	15.14
Corn		
Hippodamia convergens	0	0
H. tredecimpunctata tibialis	0	0
H. parenthesis	3.82 (0.89)	4.17 (0.97)
Coleomegilla maculata lengi	0	0
Cycloneda munda	2.90 (0.87)	3.04 (0.91)
Coccinella transversoguttata richardsoni	2.90 (0.87)	7.51 (0.78)
A. binpunctata	3.77 (0.88)	5.06 (0.92)
Total dissimilarity	13.39	19.77
Small grains		
Hippodamia convergens	0	0
H. tredecimpunctata tibialis	0	0
H. parenthesis	2.24 (0.92)	0
Coleomegilla maculata lengi	0	0
Cycloneda munda	5.14 (1.01)	5.45 (0.99)
Coccinella transversoguttata richardsoni	4.62 (1.07)	7.80 (0.80)
Total dissimilarity	12.00	13.25

* *R*-statistic differs significantly from zero (α=0.05)

(α=0.05) (Table 4), indicating that community structure differed in each crop among the two 5-year time periods, one prior to invasion and the other after invasion. *R*-statistics for the 1974–1978 with 1981–1985 comparison were not significant for any crop; thus there was no evidence to indicate that communities differed among the two 5-year periods prior to C7 invasion. Presence of slightly negative *R*-statistics for 1974–1978 with 1981–1985 comparisons indicates that there was slightly greater similarity in community structure among years from different five-year groupings than there was among years from the same group of 5 years; however *R* did not differ significantly from zero for the comparisons. In each crop, total Bray-Curtis dissimilarity was greater for the comparison of pre- versus post-invasion periods than it was for pre- versus pre-invasion periods (Table 4). *C. transversoguttata richardsoni* accounted for a large fraction of the increase in dissimilarity in all crops, however other species such as *C. munda* and *H. tredecimpunctata tibialis* also contributed.

A comparison of communities in each crop using the entire series of 13 years' data prior to invasion and 5 years after invasion yielded *R*-statistics of 0.31, 0.38, and 0.14 for alfalfa, corn, and small grains, respectively, all of which differed significantly from zero. Results of *R*-tests based on all available data were consistent with previous tests, i.e. there were significant differences in the structure of pre- versus post-invasion coccinellid communities in alfalfa, corn and small grain fields in eastern South Dakota. Variation in abundance of *C. transversoguttata richardsoni* accounted for the greatest contribution to total Bray-Curtis dissimilarity between pre- and post-invasion communities in all crops (35–53%) (Table 5); while *A. bipunctata* accounted for a large fraction (32%) of total dissimilarity in corn.

Durbin-Watson statistics were calculated to test for serial correlation in species annual abundance time series. Data spanning the two year gap (1986–1987) during which populations were not monitored were of no value for estimating autocorrelation at time lags of less than 3 years, and would thus be expected to reduce the power of the Durbin-Watson test. Consequently, only species annual abundance data from the 13 years prior to invasion

Table 5 Average contribution of each native coccinellid species to Bray-Curtis dissimilarity in comparisons among samples from 13 years (1973–1985) prior to, with samples from 5 years (1988–1992) after invasion of eastern South Dakota by *C. septempunctata*

Species	Alfalfa	Corn	Small grains
Hippodamia convergens	0.00	0.00	0.00
H. tredecimpunctata tibialis	2.36 (0.59)	0.00	0.00
H. parenthesis	0.00	3.28 (0.58)	0.89 (0.39)
C. m. lengi	0.91 (0.40)	0.00	0.00
C. munda	4.63 (0.67)	2.85 (0.56)	4.99 (0.64)
C. t. richardsoni	6.61 (0.60)	6.38 (0.52)	6.76 (0.61)
A. binpunctata	–	5.99 (0.55)	–
Total dissimilarity	14.51	18.50	12.64

Table 6 Mean (SE) number of coccinellids per 50 sweeps in alfalfa and small grains and mean number of coccinellids per 15-min search in corn for 13 years prior to (1973–1985), and 5 years after (1988–1992), establishment of *C. septempunctata* in eastern South Dakota

Coccinellid species	Crop					
	Alfalfa		Corn		Small grains	
	Before	After	Before	After	Before	After
H. convergens	1.18 (0.24)	1.65 (0.80)	7.95 (1.71)	4.94 (3.01)	1.48 (0.21)	1.94 (0.87)
H. tredecimpunctata tibialis	0.51 (0.10)	0.21 (0.11)	5.61 (1.13)	2.23 (1.35)	0.92 (0.25)	0.33 (0.14)
H. parenthesis	0.39 (0.07)	0.37 (0.13)	0.06 (0.02)	0.24 (0.20)	0.27 (0.09)	0.35 (0.15)
C. maculata lengi	0.16 (0.03)	0.44 (0.28)	4.36 (1.37)	6.91 (3.29)	0.16 (0.04)	0.44 (0.28)
C. munda	0.01 (0.005)	0.02 (0.002)	0.06 (0.01)	0.21 (0.13)	0.03 (0.02)	0.02 (0.01)
C. transversoguttata richardsoni	0.04 (0.02)*	0.002 (0.002)*	0.29 (0.10)*	0.009 (0.009)*	0.04 (0.02)*	0.003 (0.003)*
A. binpunctata	–	–	0.04 (0.01)*	0.002 (0.002)*	–	–
Total (w/out *C. septempunctata*)	2.30 (0.28)	2.69 (0.85)	18.4 (2.35)	14.5 (4.62)	2.90 (0.43)	3.08 (1.02)
Total (with *C. septempunctata*)	–	3.31 (0.94)	–	15.8 (4.87)	–	3.84 (0.87)

* Mean abundances of a species before and after invasion differ significantly (α=0.05)

were used in conducting tests for serial correlation. Based on the 13 years' data for each species in each of the three crops a total of 19 test statistics could be calculated. None of the 19 Durbin-Watson statistics were significant (α=0.05). Thus, we concluded that abundance of a particular coccinellid species in a crop was essentially independent of its abundance in the previous year. The lack of dependence in values of a time series from one time period to the next is indicative of series composed of random deviations around an overall stationary mean value (Box and Jenkins 1976). When a stationary time series is composed of random deviations around a mean value that may have changed at a particular time due to an intervention, standard two-sample statistical tests, such as Student's *t*-test and the Mann-Whitney *U* test are appropriate for testing for differences in the mean of the time series before and after intervention. We used the Mann-Whitney *U* test because data were non-normal and sample sizes were small, i.e. 13 and 5 years. Test statistics indicated that *C. transversoguttata richardsoni* was significantly less abundant in alfalfa and corn, and *A. bipunctata* was less abundant in corn, in post-invasion years than in prior years (Table 6). Mean annual abundances of other species did not differ significantly between pre- and post-invasion periods. Even though abundances of *C. transversoguttata richardsoni* and *A. bipunctata* decreased after C7 invasion, total abundance of native coccinellids did not change significantly in any of the crops after invasion. Native coccinellid abundance was greater in alfalfa and small grains during the 5 years after invasion than in the 13 years prior to invasion, but the increases were not significant (Table 6). Even with C7 included, coccinellid abundance was not significantly greater in any crop after invasion than it had been previously (Table 6).

Discussion

Due to its broad habitat range and voracity there has been concern that C7 may pose a threat to native aphidophagous coccinellids (Staines et al. 1990; Howarth 1991). The present study suggests that this concern is justified. Results indicate that the structure of native coccinellid communities in field crops changed after C7 invaded the region of 1987, with two previously uncommon species, *A. bipunctata* and *C. transversoguttata richardsoni*, decreasing in average annual abundance by more than an order of magnitude.

This study, as with most studies of environmental impact on biological populations, does not demonstrate with certainty that competition with C7 was the cause of observed change. Causality cannot be demonstrated solely from statistical analysis of data obtained from unreplicated long-term monitoring studies (Hurlbert 1984). Our study was replicated spatially, but correlation in species abundances in a particular crop among study sites indicated that experimental replicates were not independent.

In this instance, an environmental perturbation that occurred at about the time C7 invaded eastern South Dakota and affected populations at one site would likely have had similar effects on populations at other sites.

Although, wide fluctuations in coccinellid populations were observed over the 13 years of observation prior to invasion, and populations of *C. transversoguttata richardsoni* and *A. bipunctata* had previously declined to levels as low as those recorded after invasion, they had not remained at low levels for extended periods, such as occurred after invasion. The multitude of ecological factors, other than competition with C7 that could account for observed population trends could not be measured because factors contributing to year-to-year fluctuation in coccinellid populations are not adequately understood (Elliott and Kieckhefer 1990b). Repeating the study in other regions invaded by C7 would be an obvious way of providing additional evidence regarding the influence of C7 on native coccinellids, however this is probably infeasible unless a long-term database currently exists for coccinellids in another region because C7 has already invaded most inhabitable regions of North America.

In the absence of indisputable proof, it is desirable to weigh the potential benefits of the release of a polyphagous predator such as C7 against the potential negative impacts. Even though there was a numerical increase in the abundance of predatory coccinellids in crops after establishment of C7, the increase was not significant. Thus, there was no indication that total coccinellid abundance in agricultural crops will increase as the result of addition of C7 to the fauna. Evans (1991) found that interspecific competition for food among larvae of C7 and two of the native coccinellids found in eastern South Dakota field crops (*H. convergens* and *H. tredecimpunctata tibialis*) did not differ from intraspecific competition in that an individual's weight gain did not depend on whether the competitor was conspecific or heterospecific. Furthermore aphid populations were neither more nor less reduced by larvae of two species than by an equivalent number of a single species. Evans results suggest that the presence of C7, if not accompanied by an increase in total coccinellid numbers, might result in a more diverse coccinellid species assemblage in crops, but one in which aphid predation occurs at about the same level as it did prior to invasion.

It should be pointed out that coccinellids exhibit complex interactions in agricultural landscapes related to spatial patterns of habitat use (Ewert and Chiang 1966; Honek 1985; Kieckhefer et al. 1992) as well as the seasonal timing of occurrence and reproduction in various habitats (Wright and Laing 1980; Corderre et al. 1987; Duelli 1980; Elliott and Kieckhefer 1990a, b). These factors partially determine the predatory potential of a coccinellid in a particular agroecosystem. The level of predation by a coccinellid species can also depend on the extent of overlap in the distributions of the coccinellid and aphid species on a particular plant species (Coderre and Tourneur 1986). Because of the potential for such interactions, it is difficult to predict the effect of an introduced species on biological control and on populations of native coccinellid species. However, barring major differences in predation potential among native species and C7, the absence of a statistically detectable increase in total coccinellid abundance suggests that there will not be an appreciable increase in the level of aphid biological control in the crops we studied.

Coccinellid species found in agricultural crops in eastern South Dakota are highly mobile and have broad habitat ranges. The ability of such species to survive in agricultural landscapes, which are composed mostly of habitat islands only temporarily suitable for inhabitation, is believed to be increased by landscape heterogeneity due to greater temporal continuity of suitable habitats (Duelli et al. 1990). Even though most coccinellids utilize a range of habitats, the limited information that exists suggests that species exhibit differences in the breadth of habitats occupied that vary across spatial scales (Hodek 1973; Honek 1985). For example, coccinellid species may segregate on different plant types within a particular plant community and among plant communities within a landscape (Honek 1985). Thus, if competition is an important factor structuring coccinellid assemblages, refuges from competition with C7 probably exist for most species. Differences in biology, such as degree of voltinism, may also decrease species interaction and enhance coexistence.

It is impossible to predict the eventual impact of C7 on native coccinellids in eastern South Dakota. However, the very limited information available suggests that if extinctions of species occur, they will occur at a slow rate. Effects of competition with C7 probably has reduced populations of coccinellids such as *C. transversoguttata richardsoni* in several habitats, and may also lower the rate of occupancy of available habitat patches by such species. In this case, local extinctions caused by environmental pertubations and demographic stochasticity are more likely to occur, and habitat patches are less likely to be recolonized following local extinction (Quinn and Hastings 1987; Hanski and Gilpin 1991). This may be particularly significant for coccinellids because species population fluctuations are correlated over relatively large regions (Elliott and Kieckhefer 1990a, b; Kieckhefer and Elliott 1990), which generally decreases metapopulation persistence (Harrison and Quinn 1989). It follows that coccinellid species with more specialized habitat requirements than agriculturally important species may be more susceptible to effects of competition with C7, and their populations may decline more rapidly. However, currently no information exists regarding interactions of native coccinellids with C7 in non-agricultural ecosystems in eastern South Dakota.

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