

Dynamics of Aphidophagous Coccinellid Assemblages in Small Grain Fields in Eastern South Dakota

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ABSTRACT Aphidophagous coccinellid beetle populations were sampled by sweep net from 1969 to 1985 in small grain fields in eastern South Dakota. The assemblage of coccinellids consisted of six species: *Hippodamia convergens* Guerin-Meneville, *H. tredecimpunctata tibialis* (Say), *H. parenthesis* (Say), *Coleomegilla maculata* (DeGeer), *Coccinella transversoguttata* Faldermann, and *Cycloneda munda* (Say). *H. convergens* was the most abundant coccinellid, followed by *H. tredecimpunctata*, *H. parenthesis*, *Coleomegilla maculata*, *Coccinella transversoguttata*, and *Cycloneda munda* in rank order of abundance. Seasonal patterns of population increase differed among species. At all sites, populations of each species fluctuated unpredictably among years and independently of populations of other species. Assemblage structure at a site changed unpredictably from year to year, but the extent of change was constrained. Averaged over years, there were distinct differences in the structure of coccinellid species assemblages at geographically separated sites. Although assemblage structure varied from year to year at a site, there was no evidence of systematic change in structure at any site over the years of the study. A technique was proposed for evaluating the effect of introduced predators on coccinellid species assemblages.

KEY WORDS Insecta, Coccinellidae, random walk, community

RESEARCH ON APHIDOPHAGOUS INSECTS has steadily increased over the past 20 yr as the limitations of chemical control of aphids have become apparent. This research was undoubtedly catalyzed by the success of several integrated control programs for aphids that used naturally occurring aphidophagous predators as key components of the integrated plan (Hagen et al. 1971). Aphid predators may be more effective aphid population regulators than parasitoids if prey populations are low or ephemeral and the mobile predators can opportunistically exploit alternative prey in a variety of habitats (Murdoch et al. 1985).

Species assemblages of aphidophagous coccinellid beetles (hereafter referred to as coccinellid communities) in small grain fields in eastern South Dakota are established in the spring of each year by migrants from adjacent habitats, and perhaps more distant locations, and are in a constant state of flux (Ives 1981). Development of insect communities in agricultural crops each year is influenced by the composition of the species pool of potential colonists and by the development of the habitat within the field (Liss et al. 1986). For coccinellids, the species pool of potential colonists is influenced by factors, such as availability of adequate overwintering habitat, extent of overwintering mortality,

and size of coccinellid populations entering diapause the previous autumn. The initiation and rate of colonization by a species and the ultimate size of its populations in small grain fields each year are influenced by the species' biology and life history; diapause characteristics, mobility, numerical response to prey density, and habitat requirements are among the factors that influence the timing of appearance and size of coccinellid populations in small grain fields (Honek 1986). Factors influencing habitat development include development of prey populations within the crop, weed species density and diversity, and crop plant density and phenology (through its influence on microclimate) (Honek 1986). Variable factors, such as weather, reduce the predictability of coccinellid community development through their influence on coccinellid, prey, and plant populations.

Over the past 20 years, significant changes have occurred in the character of the landscape of the 10 million ha constituting eastern South Dakota. The most dramatic of these changes was an approximately 50% reduction in land area planted to alfalfa (1.8 to 1.0 million ha in eastern South Dakota) between the early to mid-1970s and no recovery since. Area devoted to other types of hay has also declined by about 50% (0.8 to 0.35 million ha) in the trend towards intensive production of cash crops. Concomitantly, total area planted to small grains expanded by about 25% (1.9 to 2.4 million ha) before slowly declining during the 1980s to preexpansion levels. The area planted to corn was relatively stable over the 20-yr period (about

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1.5 million ha), but soybean increased about sevenfold in eastern South Dakota (to nearly 0.6 million ha). The land areas of nonagricultural lands also have changed during the past 20 years. For example, the land area of wetlands has declined steadily, and presently only 35% of the original wetland area remains (National Research Council 1982). The nature of change of coccinellid communities in small grain fields in response to the evolving landscape, through its influence on species population dynamics and species pool composition, is unknown.

Predation on aphids early in the season is potentially important in maintaining cereal aphids at low numbers during the early stages of crop development, when immigrant aphids initially colonize plants and their feeding activity can cause the greatest yield loss (Kieckhefer & Kantack 1980). Thus, the timing of initial colonization of small grain fields in the spring and rate of population increase within the crop are important determinants of a coccinellid species importance in biological control of cereal aphids in the region.

The current study was undertaken to gain insight into the development of coccinellid communities in small grain fields in eastern South Dakota both within growing seasons and among years. We compared coccinellid communities in fields at three geographically separated locations for 13 to 17 consecutive years. We searched for trends in coccinellid community structure in small grain fields among years and sites that might reflect the influence of the changing landscape on species abundances. In addition, we searched for trends in seasonal patterns of occurrence and population density of coccinellids inhabiting small grain fields to gain insight into the predictability of development of coccinellid communities and the relative importance of species as aphid predators in small grain fields.

Materials and Methods

Coccinellids were sampled in small grain fields, almost exclusively spring wheat, in eastern South Dakota throughout the growing seasons of 1969–1985. One field near Castlewood (Hamlin Co.) was sampled for coccinellids each year from 1969 to 1985. One field at each of two locations was sampled from 1973 to 1985: south of Brookings (Moody Co.) and east of Clear Lake (Deuel Co.). Fields at the same locations were sampled each year of the study. Pairwise distances among sites ranged from about 50 km between Castlewood and Clear Lake to about 80 km between Castlewood and Brookings.

Coccinellid populations in a field were sampled by collecting six subsamples, each consisting of 50 pendular sweeps (total of 300 sweeps), with a 38-cm diameter sweep net taken along transects into the field from the field edge. Insects were chloroformed in the net, transferred to containers, and taken to the laboratory where they were counted

and identified to species. Each field was sampled at approximately weekly intervals from tillering through the hard dough stage. Sampling was done in the early afternoon on sunny days, after the ambient temperature had reached at least 15°C, wind velocity was under 24 kph, and foliage was dry. Over the course of the study, the median number of 300 sweep samples taken at a site in a year was 7, the minimum was 5 and the maximum was 10.

Reliable estimates of the population densities (number/m²) of adults of all coccinellid species commonly occurring in small grain fields in eastern South Dakota can be obtained by sweep net sampling. Linear equations relating to the number of coccinellids captured per sweep in a sample of 180 sweeps with a 38-cm diameter sweep net, to the number of coccinellids/m² account for about 55 to 90% of the variance in the number of coccinellids/m², depending on species (N.C.E., R.W.K. Kieckhefer & W. C. Kauffman, unpublished data). Ambient temperature and crop growth stage influence these estimates, but their combined effect accounts for about ≤15% of the total variation in absolute density, depending on species. A large portion of the unexplained variance in estimates was probably due to sampling variability that affected sweep net and absolute density estimates (N.C.E., R.W.K., and W. C. Kauffman, unpublished data). Therefore, estimates of percentage of explained variance represent minimum estimates for 180 sweep samples. Samples of >180 sweeps should account for larger percentages of total variation. When sweep net samples are taken in small grain fields at regular intervals over the growing season, as ours were, the average number of coccinellids/m², derived from the linear equations, and averaged over all samples taken from a site in a year provides consistent, even if slightly biased estimates of the average number of coccinellids per m² during the interval of the small grain growing season over which sampling is conducted.

Minimum and maximum daily temperatures were obtained from records of the NOAA recording station nearest each site. Degree-days (DD) (Baskerville & Emin 1969) were calculated for each site each year beginning at 1 April using a lower thermal threshold of 8.9°C. This threshold was chosen as a compromise, because it is probably within 2.0°C of the true thresholds of all species (Honek & Kocourek 1988). Because degree-day accumulations using similar thermal thresholds are highly correlated (Hughes et al. 1984), use of a single threshold provides an adequate physiological time scale for all species.

To gain insight into differences among species with respect to seasonal patterns of abundance, we derived four quantitative variables from our data and subjected these derived data to multiple discriminant analysis using PROC GLM and PROC DISCRIM (SAS Institute 1985a, 433–506 and 317–334, respectively). Bartlett's (1947) statistic V (see

Table 1. Percentage of each species of the total of coccinellids collected ($n = 6,808$) and percentage of site by year samples containing each species in samples from small grain fields located at three sites in eastern South Dakota from 1969 to 1985

Species	%	
	Total	Samples
<i>Hippodamia convergens</i> Guerin-Meneville	43.8	98
<i>H. tredecimpunctata tibialis</i> (Say)	37.1	95
<i>H. parenthesis</i> (Say)	9.6	76
<i>Coleomegilla maculata</i> (DeGeer)	6.8	83
<i>Cycloneda munda</i> (Say)	0.4	30
<i>Coccinella transversoguttata</i> Faldermann	2.3	40

Dillon & Goldstein 1984, 404–405) was used to determine the number of discriminant axes from an analysis to retain. We assumed that a discriminant function provided useful information for classifying species with respect to quantitative variables if the calculated χ^2 statistic for a test was significant at the 0.05 level.

Autocorrelation coefficients were calculated using PROC ARIMA (SAS Institute 1984, 127–181) to test for dependencies from year to year in the population fluctuations of each species at each site. Kendall's tau coefficients of association were calculated using PROC CORR (SAS Institute 1985b, 861–874) for pairwise combinations of species at each site to test for dependencies in the year-to-year fluctuations of different species at the same site.

Results and Discussion

Species Composition of Coccinellid Communities. Six species of aphidophagous coccinellids commonly occurred in small grain fields in eastern South Dakota (Table 1). Aphidophagous coccinellids other than these were occasionally observed, but their combined occurrence was very infrequent, <10 individuals of any of these species were collected during the entire study. It is likely that these coccinellids were transients rather than inhabitants of the crop. *Hippodamia convergens* Guerin-Meneville and *H. tredecimpunctata tibialis* (Say) occurred at each site in nearly all years (Table 1). Four species were more sporadic occurring in 30 to 83% of site by year samples. Averaged over years and sites, *H. convergens* was the most abundant species in small grain fields, followed by *H. tredecimpunctata* (Table 1). Other species accounted for $\leq 10\%$ of all coccinellids collected.

To determine whether 300 sweep samples were large enough to characterize the species composition of coccinellid communities in small grain fields, the cumulative percentage of the total number of species collected versus the cumulative number of subsamples taken on each sampling occasion (six 50 sweep subsamples) was calculated for each sample taken from each field. An average cumulative percentage of total species collected in the sample was then calculated as a function of the number

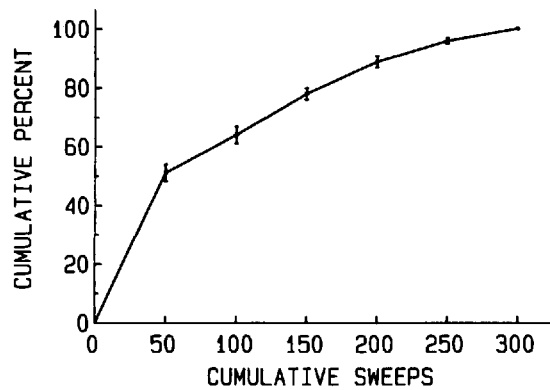


Fig. 1. Average (\pm SE) cumulative proportion of total species obtained in samples versus the cumulative number of 50 sweep subsamples taken.

of subsamples taken (Fig. 1). The curve in Fig. 1 increases only very slightly after 250 sweeps indicating that 300 sweep samples contained sufficient information to adequately characterize the species composition of coccinellid communities in small grain fields at the time of sampling.

Estimates of average annual population density were reasonably precise; average (averaged over the 43 site-by-year data sets) coefficients of variation (standard error/mean) of population density estimates ranged from 0.05 (SE = 0.01) for *H. convergens* to 0.16 (SE = 0.03) for *Cycloneda munda* (Say). Because several 300 sweep samples were taken from the same field over the course of a growing season and were therefore not independent, the coefficients of variation measure both sampling variability and seasonal variation in population density, and therefore overestimate the magnitude of sampling error. Thus, our estimates of average annual population densities, based on approximately seven 300 sweep samples taken at regular intervals throughout the growing season provided reliable estimates of average population densities of coccinellids in small grain fields and of community composition, and permit comparison of populations and communities from year to year and field to field.

Seasonal Patterns of Community Development. Coccinellids were present in small grain fields throughout most of each growing season (Fig. 2). Three species, *H. convergens*, *H. tredecimpunctata*, and *Coleomegilla maculata* (DeGeer), were frequently present in the crop at detectable levels during the tillering stage of plant growth.

Our objective in subjecting our data to discriminant analysis was to classify species according to population density and seasonal pattern of population change based on samples of each species from each site each year.

We derived four quantitative variables from our data that captured salient features of population density and seasonal pattern of population growth: (1) the cumulative number of degree-days at which

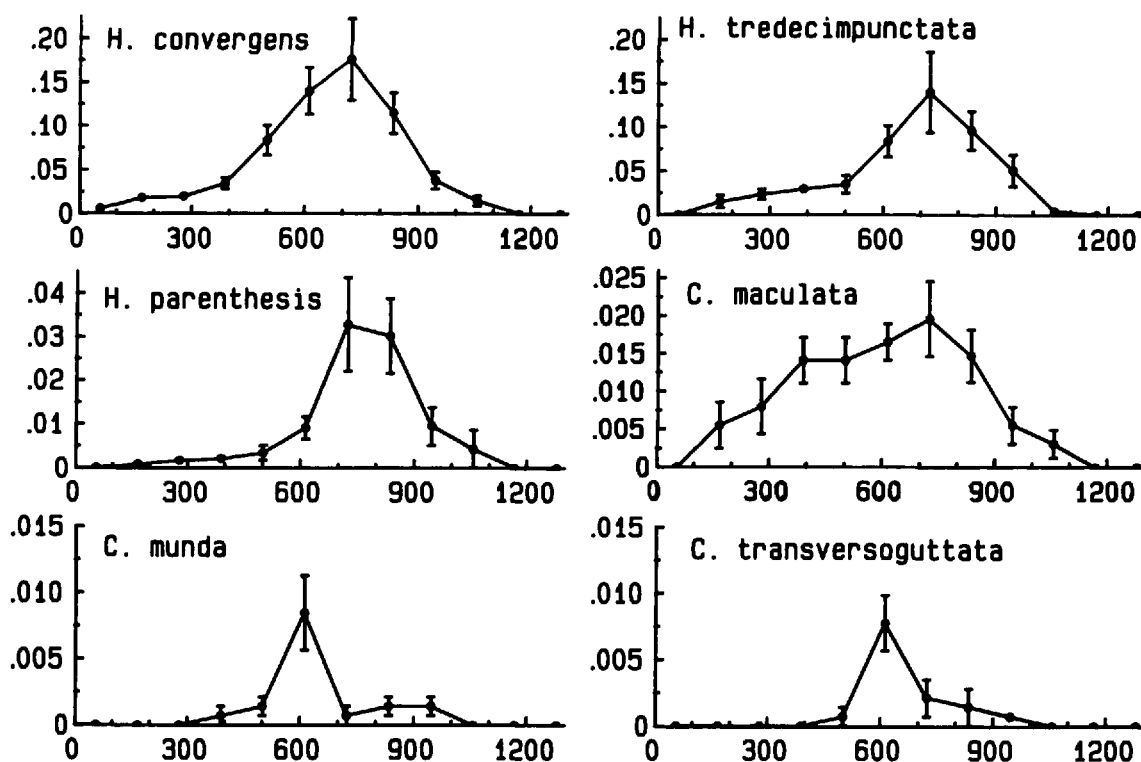


Fig. 2. Average (\pm SE) number of coccinellids/m² in small grain fields throughout the growing season. Data are averages from three sites sampled from 13 to 17 yr each. To facilitate pictorial representation, samples were grouped at 111 DD intervals (1-111, 112-222 DD, etc.) and each sample in an interval was considered to have been taken at the midpoint of the interval. Vertical bars on data points are standard errors.

the first sample containing the species was taken; (2) the cumulative number of degree-days at which the median of the species cumulative population density distribution, e.g., 50% of total population, occurred; (3) the average population density of the species at a site in a year; and (4) the average population density of the species during the early portion of the growing season (<450 DD). In an average year, 450 DD had accumulated by about mid-June and spring small grains were typically nearing the boot stage of development by that date.

Only the first and second discriminant functions provided significant information for classifying species with respect to the quantitative variables. The eigenvalues, V statistics, and coefficients of significant discriminant functions are listed in Table 2. The first discriminant function can be given

the following interpretation: species with high scores were those that colonized the crop early in the season, and whose populations increased to high levels early in the season and attained high average densities. Species with low scores colonized the crop later in the season and achieved low population densities. The second function has a less straightforward interpretation. Species obtaining high scores on the second function generally were those that colonized the crop late, those that attained high average population densities, or those that displayed both these characteristics.

Centroids for each species in the coordinate system formed by the two discriminant functions are illustrated in Fig. 3. Species appear to fall into three groups, one containing *H. convergens* and *H. tredecimpunctata*, one containing *C. maculata*, and

Table 2. First two discriminant functions for classifying six coccinellid species using four quantitative variables describing population density and temporal patterns of occurrence of coccinellids in small grain fields

Function	Eigenvalue	V	Coefficients ($\times 10^2$) variable			
			1	2	3	4
I	0.771	140.6 ^a	-0.0226	-0.00222	19.4	116
II	0.087	23.9 ^a	-0.0412	-0.00486	-36.6	105

Eigenvalues of the first two functions and V statistics (Bartlett 1947) are also listed.

^a $P < 0.05$.

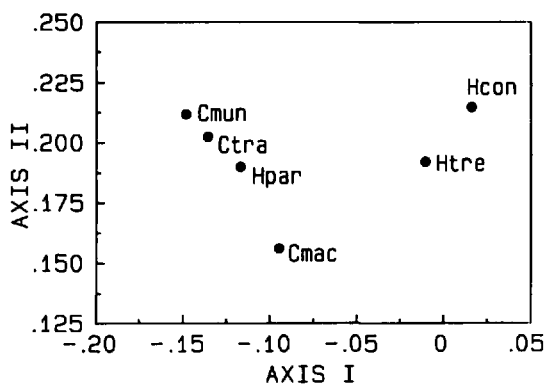


Fig. 3. Centroids for each coccinellid species on the first two discriminant axes (eigenvalues are 0.771 and 0.087). Cmun, *Cycloneda munda*; Ctra, *Coccinella transversoguttata*; Cmac, *Coleomegilla maculata*; Hcon, *Hippodamia convergens*; Htre, *H. tredecimpunctata*; Hpar, *H. parenthesis*.

a third containing the remaining species. Within these three groupings, the proportion of misclassified observations is high, but the proportion of species belonging to one group classified as members of another group is lower (Table 3). The results indicate that differences exist among species in both the timing and extent of colonization of small grain fields. The relatively high proportion of misclassified observations indicates that species vary markedly over time with respect to patterns of colonization and population density.

Patterns of Population Change. At all sites, populations of each species fluctuated widely among years (Fig. 4). Population densities of *H. convergens* varied least, in a proportional sense, approximately one order of magnitude, whereas *Cycloneda munda* and *Coccinella transversoguttata* Falderman were virtually absent from the crop at individual sites in several years.

The population density of a species at a site appeared to be unrelated, or weakly related, to the population density of that species at the same site in adjacent years (Fig. 4). To determine whether significant autocorrelation existed among densities of conspecific populations at a site, we calculated autocorrelation coefficients at a time lag of 1 yr from time series of population density data for each species at each site (total of 18 autocorrelations). The average of negative autocorrelations was -0.12 ($n = 8$) and the average of positive autocorrelations was 0.25 ($n = 10$); only one coefficient differed significantly from zero ($P < 0.05$), that being for *Coleomegilla maculata* at Castlewood ($r = 0.59$). Although we might not expect many significant autocorrelations, because our time series were relatively short (13–17 yr), we would expect autocorrelations to be of relatively large magnitude if populations of a species at a site exhibited strong dependencies from year to year. The general absence of large autocorrelations suggests that pop-

Table 3. The proportion of site-by-year samples of coccinellid species misclassified as other members of the same group (diagonal elements) and as members of another group (off-diagonal elements) based on discriminant analysis of six coccinellid species using five quantitative variables

Group	Group		
	1	2	3
1	0.30	0.22	0.04
2	0.14	—	0.26
3	0.03	0.16	0.43

Group 1, *H. convergens*, *H. tredecimpunctata*; Group 2, *C. maculata*; Group 3, *H. parenthesis*, *C. munda*, *C. transversoguttata*.

ulations of all species at a site fluctuate unpredictably from year to year.

Similarly, populations of different species at the same site appeared to fluctuate nearly independently of one another (Fig. 4). To formally test this observation, Kendall's tau coefficients of association were calculated for pairwise combinations of species at each site (3 sites by 15 pairwise combinations of species). Only 4 of 45 Kendall's tau statistics differed significantly from zero ($P < 0.05$). An average of 2.3 out of 45 significant statistics would be expected simply by chance at our chosen significance level. Thus, there was only limited evidence of synchrony in the population fluctuations of different species at the same site. This result was somewhat surprising to us, because we thought that species might respond numerically in similar fashion within years at a site, perhaps in response to annual fluctuations of aphid populations at the site.

Patterns of Community Change. Analysis by ordination is a useful means of summarizing coccinellid community patterns over time and space. Ordination is a generic name for data reduction techniques in which samples are arranged along one or more coordinate axes (usually two axes) such that their relative positions with respect to the axes provide information about the similarities in species abundances among samples (Gauch 1982). Ideally, samples that are most similar to each other in species composition will be those most similarly positioned in the space defined by the coordinate axes, and those most dissimilar will be most distant from one another. Correspondence analysis (COA) is a commonly used ordination technique that generally results in ordinations that faithfully depict the ecological similarities among samples from communities (Gauch 1982). Samples from individual sites and years were ordinated using COA. The ordination space derived from the COA of our 43 site-by-year data sets, each set representing the average population density of each species at a single site in a single year, provided an approximation of the sample space of possibilities for coccinellid community structure in small grain fields in eastern South Dakota. The two-dimensional coordinate

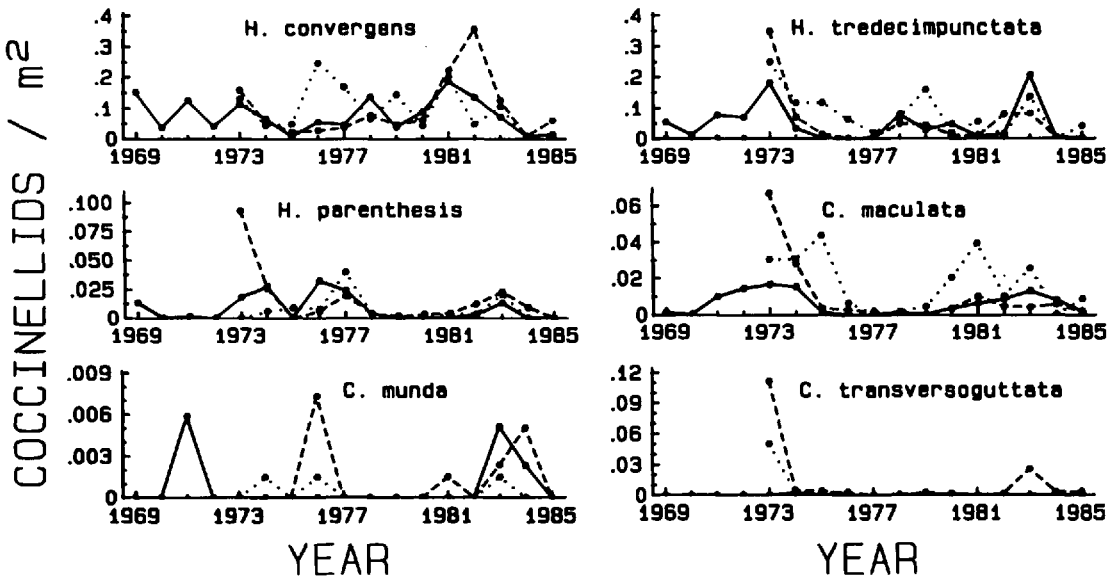


Fig. 4. Average number of coccinellids/m² in small grain fields at three sites in eastern South Dakota in each of 13 yr (Brookings and Clear Lake) and 17 yr (Castlewood). Brookings, dotted line; Clear Lake, dashed line; Castlewood, solid line.

system defined by the first two nonunitary eigenvectors of the COA provided a graphical representation of change in coccinellid communities among years at individual sites and among geographically separated sites (Fig. 5). It may be helpful to bear in mind that our purpose in analyzing these community ordinations is to search for pattern in community change over time and space; we distinguish this objective from that of determining the mechanisms underlying change in community structure.

The location in ordination space of communities at a site changed markedly among successive years and exhibited little visual evidence of pattern in either the euclidian distance moved or the direction of movement of local communities among successive years at a site (Fig. 5). A one-way analysis of variance of data from 1973 to 1985 indicated that the distance moved by local communities from one year to the next differed significantly among pairs of consecutive years ($F = 7.85$; $df = 11, 24$; $P = 0.0001$). Distances moved in ordination space by local communities among successive pairs of years can be viewed as time series of observations on the extent of community change from year to year. Autocorrelation coefficients were calculated for a time lag of 1 yr for each time series of community displacement data, one from each site. There was no significant ($P < 0.05$) autocorrelation among distances moved in ordination space by communities at any site, autocorrelation coefficients were -0.07 for Brookings, -0.12 for Clear Lake, and -0.51 for Castlewood.

Although there was considerable overlap in the regions of ordination space occupied by communities at a site, data from each site appear to be

concentrated in slightly different regions within ordination space (Fig. 5); this observation was verified by analysis of variance. Average coordinates on ordination axis I (averages for years 1973–1985) did not differ significantly among sites ($F = 1.54$; $df = 2, 36$; $P = 0.23$), but average coordinates on axis II did differ ($F = 3.71$; $df = 2, 40$; $P = 0.03$). To determine if communities at different sites tended to move similar directions and distances from one year to the next within the two dimensional ordination space, we computed coefficients of redundancy (see Dillon & Goldstein 1984, 350–352) from the bivariate time series of COA coordinates of communities at each of the three sites. Redundancy coefficients varied among pairs of sites; patterns of year-to-year movement within ordination space of communities at Clear Lake and Castlewood were similar ($R^2 = 0.64$, $P = 0.01$), whereas movement patterns at these sites did not exhibit detectable similarity to those of communities at Brookings, $R^2 = 0.31$ and 0.28 ($P > 0.05$ for both) for pairwise comparisons.

When viewed over many years, it becomes apparent that coccinellid communities in small grain fields at geographically separated sites occupy overlapping but nonidentical subspaces of a total ordination space. However, communities vary extensively among years at all sites and the extent of change in community structure at a site from year to year, and consequently, community structure itself are quite unpredictable. Year-to-year change in community structure at two sites tended to be similar in magnitude and direction suggesting that some determinants of coccinellid community structure exhibit a degree of constancy over large geographic areas.

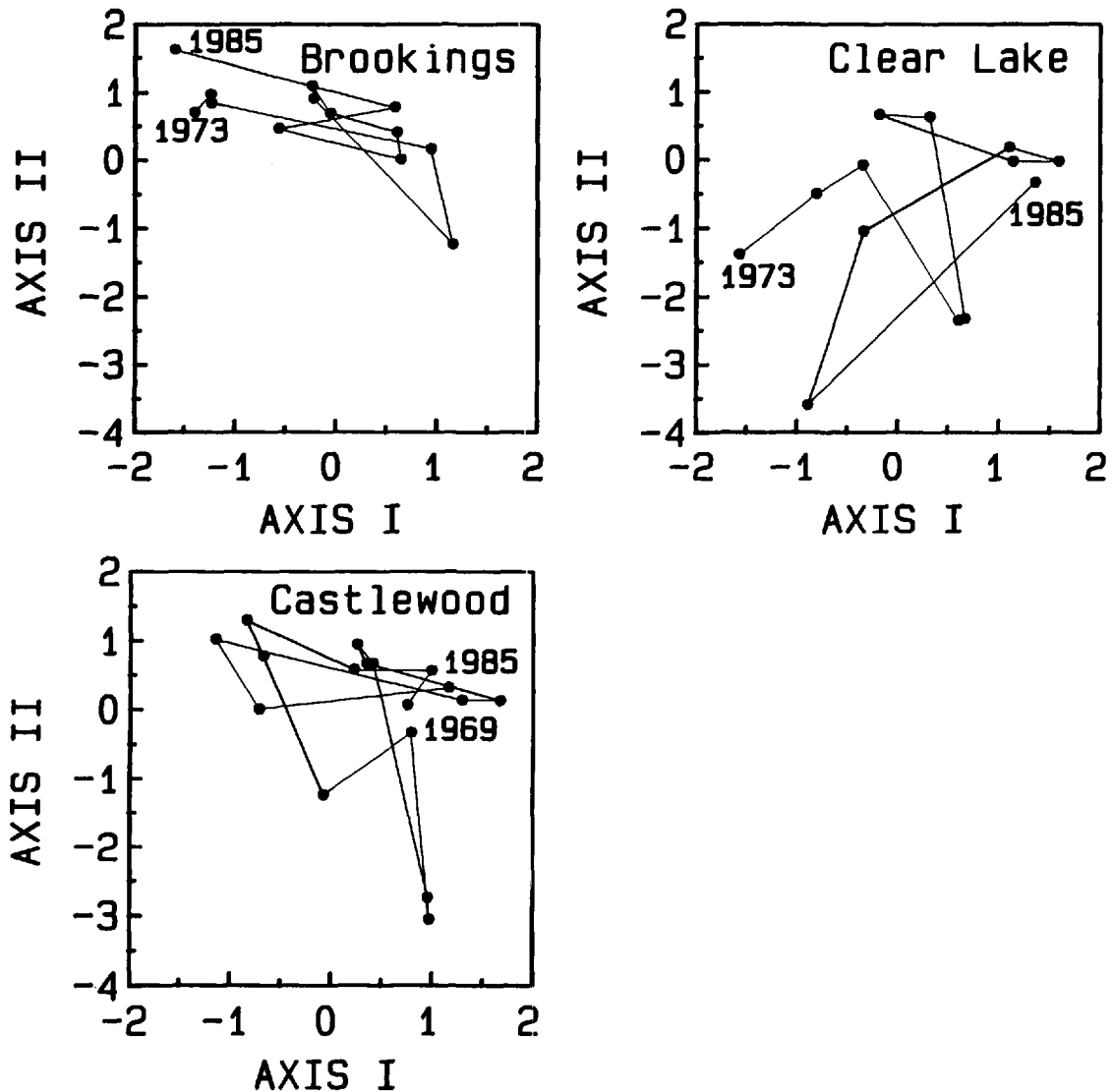


Fig. 5. Positions of coccinellid communities in COA ordination space in 13 consecutive years (Brookings and Clear Lake) and 17 consecutive years (Castlewood). Results for each site are graphed in the ordination space generated from a single COA analysis of data from all sites. Eigenvalues of axes I and II are 0.221 and 0.118, respectively.

Coccinellid Community Change Systematic or Random? The unpredictability of local coccinellid populations suggests that communities develop in small grain fields each year from a pool of species, the composition of which changes unpredictably within limits on the extent to which population densities of species can change from one year to the next; these limits may be imposed by the biotic and abiotic environment at a site. The primary determinants of population fluctuations of species, and hence, species' pool composition likely proceeds outside small grain fields, perhaps in overwintering sites where species may be differentially subject to mortality, or in alternative habitats where species feed, reproduce, and interact with one another. Stochasticity in colonization dynamics, fe-

cundity, and survival may further decrease the predictability of coccinellid community development in small grain fields. The net result would be apparent random change in structure of local communities among years, but varying degrees of coupling of community dynamics among geographically separated fields.

We sought to determine if the structure of coccinellid communities had changed appreciably from 1969 to 1985, and if so, whether this change was systematic, perhaps reflecting concomitant changes in the landscape of eastern South Dakota, or whether community change over time was essentially random, i.e., dominated by stochasticity in population fluctuations of its species. Evans (1988) observed what appeared to be random change among

years in the composition of grasshopper communities in tallgrass prairie. He proposed as a null hypothesis to account for this change that fluctuations in grasshopper communities in tallgrass prairie from year to year represented random movement of grasshopper communities among states in an ordination space of all possible states and, therefore, could be described mathematically as a two-dimensional correlated random walk within the space. Evans (1988) and Kareiva & Shigesada (1983) give a justification for applying the random walk hypothesis to community dynamics, and a detailed recipe for testing the hypothesis, respectively. We applied this test to determine if year-to-year movement within ordination space by coccinellid communities in small grain fields could be adequately described as a random process, i.e., a correlated random walk.

It is well known that an entity undergoing a random walk will drift away from its initial position as time proceeds (Kareiva & Shigesada 1983). The movement of a community undergoing a random walk in ordination space is governed by probabilistic rules that determine its displacement, or more precisely, squared displacement from an initial point. From empirical probability distributions of move lengths and turning angles between successive moves, expectations of functions of these random variables can be estimated and used to estimate expected net squared displacement of the community within ordination space (Kareiva & Shigesada 1983). The location of the community in ordination space will change from year to year according to probabilities governing both the turning angle between successive moves and displacement distances; these probabilities are independent of the current state (structure) of the community. Such a community will show no more tendency to return to a characteristic state from states far removed from that state than it will from states close to it. In other words, the community will display no feedback mechanisms or memory of its prior states. As indicated above, constraints on movement of communities from year to year in ordination space arise from the limits on the extent to which species populations can change from year to year and from the distribution of possible states that the community can occupy. These constraints are implicit in the probability distributions of move lengths and turning angles. With this analysis, it is impossible to determine whether communities themselves are void of stochastic fluctuations and change is simply a reflection of stochasticity in the processes governing community change, or whether community dynamics have a purely stochastic component that is unrelated to any controlling processes. However, this limitation is unimportant to our analysis, because we are primarily interested in the pattern of community change over time.

The random walk model predicts that the net squared displacement of communities from an initial point (their positions in ordination space in

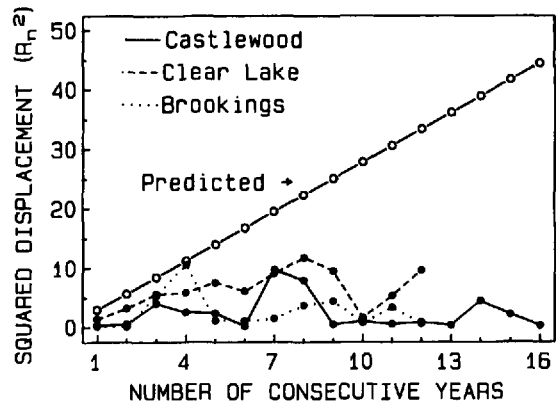


Fig. 6. Squared displacements, in COA units, of coccinellid communities from their initial positions after 1 to 12 yr (Brookings and Clear Lake) and 1 to 16 yr (Castlewood), compared with predictions from a correlated random walk model.

1969 for Castlewood and in 1973 for Brookings and Clear Lake) will increase steadily with time, i.e., with the number of successive years separating observations (Fig. 6). The actual squared displacements of coccinellid communities from their initial locations in ordination space changed continually, but contrary to the prediction of the random walk model, communities exhibited no tendency to drift away from their initial positions (Fig. 6). Even though the structure of the coccinellid community that developed at a site in a year was unpredictable, communities were limited to only a subspace of the total state space. Thus, the forces structuring coccinellid communities were probably also bounded; coccinellid community development can therefore be considered predictable in the sense that communities fluctuate within limits imposed by the biotic and abiotic environment at a site.

General Discussion and Conclusions

Differences existed among coccinellid species in seasonal patterns of population increase and average population densities within small grain fields. Species that attain large populations early in the growing season may play an important role in maintaining cereal aphid populations at low levels while plants are in the early stages of growth, during which relatively low numbers of cereal aphids can reduce yield (Kieckhefer & Kantack 1980). Although we recognize that factors other than timing of colonization and population density are important in determining the predatory potential of coccinellids, based solely on the results of our analysis, *H. convergens* and *H. tredecimpunctata* were the most important coccinellid predators of cereal aphids in small grains in eastern South Dakota over the 17 yr of our study. Populations of these species fluctuated unpredictably and independently among

years, and as a consequence, the importance of each species varied among years at individual sites. The timing and extent of colonization of small grain fields by all species varied greatly among years, and species other than these two occasionally dominated the aphidophagous coccinellid community at individual sites.

Coccinellid communities at geographically separated sites differed with respect to their average community structure. Factors associated with the landscape surrounding small grain fields at different locations may have influenced the composition of the pool of coccinellid species available to colonize the crop. The availability of adequate overwintering habitat and suitable alternative habitats for coccinellids may influence the number of species colonizing small grain fields and their population densities (Honek 1986). A challenge for future research will be to identify the complex relationships between coccinellids and features of the surrounding landscape. Knowledge of these relationships may allow us to manipulate the landscape in ways that increase coccinellid populations available to colonize agricultural crops. On the other hand, within the limits set by the nature of the biotic and abiotic environment at a particular site, species population dynamics, and consequently community structure, are largely unpredictable among years. This unpredictability probably results from the influence of variable factors such as weather on both coccinellid populations and the development of suitable habitat within the field, for example the development of aphid populations. Understanding the determinants of coccinellid population dynamics may permit prediction of the extent of biological control to be expected in a given year. In addition, determining relationships between coccinellid community development and development of the habitat within small grain fields may lead to the development of crop management practices that improve our ability to promote biological control by these natural enemies.

There was no evidence of systematic change in coccinellid communities over the 17 yr of our study. Changes in cropping and land use patterns apparently had no net effect on populations of aphidophagous coccinellids that colonize small grain fields in eastern South Dakota. These results are of interest to the problem of evaluating the effect of recently introduced exotic aphidophagous coccinellids on native species (Obrycki et al. 1987). Assuming coccinellid communities in small grain fields are exhibiting no net change in their characteristic structure over time, year-to-year change is not precluded, a test of the effect of newly established species on native species could be constructed by asking whether the coordinates in ordination space of a community of native species (excluding introduced species) sampled at one or more of our sites by our methods are consistent with those of previous communities at the site(s). A formal statistical test could be constructed by determining the prob-

ability that the ordination coordinates of the community are consistent with those of a community drawn randomly from a bivariate probability distribution, the parameters of which are estimated from the ordination coordinates of previously sampled communities at the site(s).

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