

THRESHOLD EFFECTS OF LANDSCAPE STRUCTURE ON BIOLOGICAL CONTROL IN AGROECOSYSTEMS

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Abstract. Habitat fragmentation may adversely affect the ability of natural enemies to control pest outbreaks in agricultural landscapes by interfering with their search behavior and ability to aggregate in response to prey. We determined how landscape structure affected the ability of two ladybird beetles (Coleoptera: Coccinellidae) to track aphid populations in experimental landscapes that differed in the abundance and degree of fragmentation of red clover (*Trifolium pratense*). One coccinellid was a native species (*Coleomegilla maculata* Pallas) and the other (*Harmonia axyridis* Timberlake) was introduced specifically for the biological control of crop pests such as pea aphids (*Acyrtosiphon pisum* Harris; Homoptera: Aphididae).

Landscape structure exhibited a threshold in lacunarity (a measure of interpatch distances) below 20% habitat, at which point clover patches became significantly more isolated. This threshold in landscape structure was mirrored by a similar threshold in the distribution of pea aphid populations. The distribution of the biocontrol agent, *H. axyridis*, tracked this threshold in aphid distribution, but the native coccinellid, *C. maculata*, was unable to do so in fragmented clover landscapes. Although *C. maculata* was a more active forager within clover cells, overall it was less mobile and moved significantly less among clover cells and between landscapes than *H. axyridis*, which may have contributed to its inability to track aphid populations in fragmented landscapes. The two coccinellids did not differ in their search success within fragmented landscapes, however, and it was only in clumped landscapes that *H. axyridis* maximized search success and foraged within clover cells that had 2.5–3 times more aphids than those in which *C. maculata* occurred.

Thus, the potential of predators to control pest populations in fragmented landscapes may ultimately reflect the extent to which thresholds in landscape structure interfere with the aggregative response of predators. In this system, the aggregative response of coccinellids was more closely tied to thresholds in the distribution of clover than aphids. With its greater mobility, *H. axyridis* was more effective than the indigenous *C. maculata* at tracking aphids when they occurred at low patch occupancy (below the threshold in landscape structure), which is a requisite for successful biocontrol. If native insect predators are generally more sensitive to habitat fragmentation, greater reliance may be placed on the introduction of exotic species for biocontrol, which is not without economic cost and potential ecological impacts to native insect communities. Our study demonstrates that, in addition to economic thresholds, there are also ecological thresholds that must be surmounted if biocontrol measures are to be successful. In addition to enhancing vegetational diversity within agroecosystems, conservation biological control should also strive to mitigate fragmentation effects on natural enemies, especially if thresholds in landscape structure disrupt predator–prey interactions and compromise the efficacy of biocontrol programs.

Key words: aphids; coccinellids; conservation biological control; experimental model systems; fractal landscapes; habitat loss and fragmentation; landscape ecology; movement behavior; predator–prey interactions.

INTRODUCTION

Habitat loss and fragmentation are becoming a serious impediment to the biological control of insect

pests, particularly within managed systems such as agroecosystems. Habitat fragments support a less diverse community of natural enemies, resulting in lower predation or parasitism rates on pest populations (Kruess and Tscharrntke 1994, Roland and Taylor 1997) which may release insect pests from control by their natural enemies, thus increasing the potential for economically devastating outbreaks in fragmented landscapes. Understanding how landscape structure affects species interactions, and determining the scale at which such interactions occur relative to the scale of habitat

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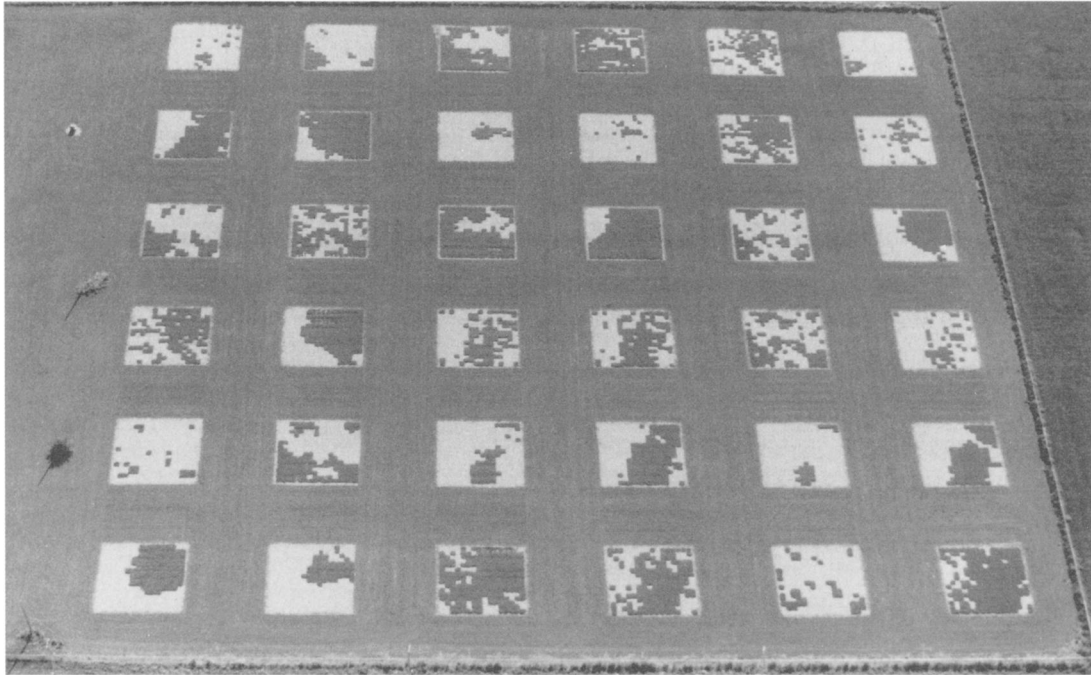


FIG. 1. Experimental model landscape system created to study the effect of landscape structure on predator–prey interactions in red clover. Each plot (16×16 m) represents a landscape pattern generated as a fractal distribution of clover at one of six levels of habitat abundance (10%, 20%, 40%, 50%, 60%, and 80%) and two levels of fragmentation ($H = 1.0$, clumped; $H = 0.0$, fragmented).

fragmentation, is critically important for the implementation of effective biocontrol programs (Roland and Taylor 1997, Thies and Tscharntke 1999). Although spatial structure or heterogeneity has traditionally been considered to have a stabilizing effect on predator–prey interactions (e.g., Hilborn 1975, Hastings 1977, May 1978, Taylor 1988, Hassell et al. 1991, Murdoch et al. 1992), these dynamics may become destabilized, resulting in pest outbreaks, if habitat fragmentation occurs at a scale that interferes with predator search behavior. For example, aphid outbreaks occurred with greater frequency and intensity within individual goldenrod patches in a fragmented system, presumably because the scale of fragmentation (1 m) was sufficient to interfere with the search behavior and foraging efficiency of ladybird beetles, thus affecting their ability to aggregate within patches (Kareiva 1987, 1990). The relationship between individual search behavior and population aggregation has not been well established (Ives 1995), however, despite the conviction that high search efficiency leading to a spatially aggregated attack is the key to successful biological control (Murdoch and Briggs 1996).

What levels of habitat loss and fragmentation are likely to interfere with predator movement or search behavior? Simulations on theoretical landscapes (neutral landscape models) revealed that search success declined abruptly when habitat fell below 20% (With and King 1999a). Interestingly, this threshold in search suc-

cess did not coincide with thresholds in habitat connectivity (percolation thresholds), but with thresholds in the gap structure (interpatch distances, or lacunarity) of landscapes (With and King 1999a). Coincidentally, tenebrionid beetles (*Eleodes obsoleta*) and small crickets (*Acheta domestica*) searching for habitat in experimental landscapes exhibited threshold responses in certain movement parameters when habitat fell below 20% (Wiens et al. 1997, With et al. 1999). Furthermore, parasitism rates have been found to decline in agricultural landscapes when the noncrop area fell below 20% (Thies and Tscharntke 1999), to levels (32–36%) below which successful biological control can occur (Hawkins and Cornell 1994). Collectively, these studies suggest that there may exist thresholds in landscape structure that interfere with search efficiency and the ability of natural enemies to aggregate and control insect pests.

To test this hypothesis, we created experimental landscapes of red clover (*Trifolium pratense* L.) across a gradient of habitat abundance and fragmentation (Fig. 1) to determine (1) whether thresholds in landscape structure precipitate similar thresholds in the distribution of an insect pest, the pea aphid (*Acyrtosiphon pisum* Harris; Homoptera: Aphididae); and (2) how landscape structure affects the search behavior of two species of aphidophagous ladybird beetles (Coleoptera: Coccinellidae). One coccinellid, *Harmonia axyridis* (Pallas), was introduced as a biocontrol agent of scale

and aphid pests throughout the eastern United States and has become established throughout this region in the past decade (Chapin and Brou 1991). The other coccinellid, *Coleomegilla maculata* (Timberlake), is indigenous and preys upon aphids, but may also consume plant pollen (Maredia et al. 1992). And, (3) what levels of habitat loss and fragmentation affect the ability of these natural enemies to track and potentially control aphid populations?

STUDY AREA AND METHODS

Experimental model landscape system

We created an experimental model landscape system (EMLS) to study how habitat abundance and fragmentation affect arthropod diversity and species interactions (predator-prey and host-parasitoid relationships). Our EMLS was established on a 4-ha site at the Bowling Green State University Ecology Research Station in May 1997 (Fig. 1). Note that we define "landscape" in a general sense, as a spatially heterogeneous area (Turner 1987) that is scaled relevant to the process or organism under investigation (Wiens 1989). The use of experimental model systems for investigating the effect of spatial pattern on ecological processes has become an important tool in landscape ecology (Wiens et al. 1993, Ims 1999).

The design of our EMLS was inspired by percolation theory and its neutral landscape model derivatives (With 1997, With and King 1997). Landscape patterns were first computer generated as fractal distributions of habitat using the midpoint displacement algorithm (Saupe 1988) to produce grid-based maps (landscape grid: 16×16 cells = 256 cells total). A fractal algorithm was used to generate landscape patterns because this permitted simultaneous control over both the abundance and spatial contagion of habitat across a fragmentation gradient (With 1997). Fractals represent the "geometry of nature" (Mandelbrot 1983) and thus our intent in this experiment was to create realistic landscape patterns that would permit us to explore in a general way how aspects of landscape structure (e.g., habitat connectivity) affected predator-prey relationships, rather than to explore how specific cropping systems or different agrolandscape designs might alter these relationships. Three replicate maps were generated for each landscape pattern, a combination of habitat abundance (six levels: 10, 20, 40, 50, 60, 80%) and spatial contagion (two levels: clumped, $H = 1.0$ and fragmented, $H = 0.0$), for a total of 36 landscape maps. We then recreated these fractal landscape patterns in the field by randomly assigning one of the computer-generated maps to each of the 36 plots, and then planted medium red clover according to the specified fractal design for that plot (plot: 16×16 m, each cell = 1 m^2). Plots were meticulously maintained throughout the growing seasons (May-September) in 1997 and 1998 to preserve landscape patterns through a combination

of periodic herbicide application in nonclover cells and by hand-weeding clover cells. The intervening matrix between plots (plots were separated by 16 m) was tilled as needed to control weeds (approximately every 2-3 wk). Colonization of these experimental plots by arthropods was through natural immigration. Aphids and both coccinellid species were present on these plots within two months of planting the clover and thus populations were well established during the second season when this study was conducted.

The scale of these landscapes (16×16 m) should be adequate for studying predator-prey interactions and the effects of fragmentation on these interactions, especially considering that studies addressing similar types of questions in agroecosystems have focused on linear arrays or plots that were considerably smaller than the dimensions of our plots (e.g., 1×20 m, Kareiva 1987; 5×5 m and 5×10 m, Ives et al. 1993; 2×32 m, Banks 1999). Furthermore, the spatial grain of our experiment (1-m^2 clover cells) is commensurate with the scale of habitat patches studied by other investigators in agroecosystems (e.g., Kareiva 1987, Kruess and Tsharntke 1994). Thus, if a landscape is defined as a collection of habitat patches, then these plots represent landscapes given the scale of patchiness that affects predator-prey dynamics in this system. Although our plots were not completely isolated in that individual coccinellids could (and did) move between them (cf. Table 6), the distance separating plots (16 m) in our EMLS is, again, greater than or similar to other experimental studies that addressed fragmentation effects on predator-prey interactions for coccinellids in agroecosystems (e.g., 1 m between arrays in Kareiva 1987; 3-5 m between arrays in Banks 1999; 20 m between plots in one of the experiments reported in Ives et al. 1993).

Species distributions in fractal landscapes

The distributions of pea aphids and the two coccinellid species within each landscape were assayed during general arthropod surveys conducted by D. M. Pavuk during 1-14 June (first survey) and 28 June-12 July (second survey) 1998. Surveys were completed within a 2-wk period to minimize temporal variation in the occurrence and abundance of species across the study area. Each clover cell was visually inspected for ~ 1 min and all species present were recorded. It took as little as 20 min to survey all clover cells in a 10% landscape and as much as 3.5-4 h to survey each 80% clover landscape (~ 205 clover cells). We used these survey data to generate distribution maps for pea aphids and the two coccinellids in each landscape (i.e., map of the clover cells occupied by each species in a given landscape).

Effect of landscape structure on species distributions

The landscape and species distribution maps were subjected to a lacunarity analysis using the gliding-box

algorithm (Allain and Cloitre 1991). Lacunarity analysis quantifies the variability in the distribution of gap sizes (distances among clover or occupied cells) at different scales. Lacunarity is derived from fractal geometry, but is basically a variance-to-mean ratio and is thus similar to measures of aggregation such as Morisita's Index (Plotnick et al. 1993, 1996). The lacunarity index (Λ) of landscape pattern has been shown to be a good descriptor of search success for simulated organisms on fractal landscapes (With and King 1999a), and has recently been used as a measure of "landscape function" to relate patterns of space use by organisms (tenebrionid beetles) to experimental landscape patterns (McIntyre and Wiens 2000).

To determine the relationship between landscape pattern and species distributions during the first survey, we conducted a full-factor analysis of variance (ANOVA) to determine how the lacunarity of species' distributions (Λ) varied among species (clover, pea aphids, *H. axyridis*, and *C. maculata*) and as a function of habitat abundance (six levels) and spatial contiguity (clumped vs. fragmented), with a Type III sums of squares for unequal replication (i.e., insect species were absent from some plots). Although these three species were known to occur on all plots during the first survey, they may have been overlooked or were absent on the particular day a given plot was surveyed. Thus, plots in which the species was not recorded are treated as "missing values" in all analyses for this first survey. As with most landscape metrics, the ability to detect pattern using the lacunarity index is dependent upon the scale of analysis, which is defined by the spatial grain or "window size" of the analysis (e.g., scale 2 is a 2×2 -cell block). The model was significant at the first four scales of analysis (scales 1–4, $R^2 = 0.49$ – 0.72 , model $P < 0.05$; scales 5–8, $R^2 = 0.37$ – 0.43 , model $P > 0.05$), but the greatest amount of variation was explained at the second scale of analysis ($F = 4.89$, $df = 47, 89$, $P = 0.0001$, $R^2 = 0.721$). Thus, results obtained at this scale (2×2 m²) are presented and discussed throughout the paper. Significant differences among means were determined by Tukey hsd tests. The relationship among the distributions (Λ) of these various species was additionally explored with regression analysis (relationship between clover and aphid distributions) or multiple regression analysis with stepwise selection (P -to-enter = 0.15) to examine the relative effects of clover and aphid distributions on the distributions of each coccinellid.

Natural enemies were so effective at controlling aphids during this experiment that aphids were virtually eradicated from all clover landscapes by the second survey. This enabled us to assess what distributional patterns (based on the lacunarity index, Λ) are expected for the two coccinellids in these clover landscapes in the absence of their aphid prey. For the second survey, the full-factorial model was the same as for the first survey, but included only clover, *H. axyridis* and *C.*

maculata in the analysis of species effects. The statistical model was not significant at any scale, although about half of the variation in the data was explained by the model at each scale ($R^2 = 0.42$ – 0.48). The results for the analysis at the second scale are therefore presented for consistency with the first survey.

Cell occupancy by coccinellids

For the first survey, a full-factorial ANOVA (Type III SS) tested whether species (pea aphids, *C. maculata* and *H. axyridis*) differed in the proportion of clover cells occupied as a function of landscape structure (effects of habitat abundance and fragmentation). A separate analysis examined whether the two coccinellids differed in cell occupancy between surveys (aphids present vs. aphids absent) and as a function of landscape structure. The square root of the proportion of cells occupied was arcsine transformed prior to analysis, although qualitatively similar results were obtained from analysis of the untransformed data.

Relative effects of landscape structure and aphid distributions on predator search behavior

Except for a winged dispersal phase, aphids are apterous and are constrained to move only among host plants (Roitberg et al. 1979). They were therefore unlikely to cross gaps between clover cells once they settled on these plots, and we thus concentrated our efforts on evaluating how landscape pattern affected the search behavior of the two coccinellids. Individual ladybird beetles were found opportunistically on plots and were observed in situ for 10–60 min each (mean ± 1 SE = 28.7 ± 1.33 min for *H. axyridis*, 33.1 ± 1.29 min for *C. maculata*). On average, we observed 6 individuals/plot for each species (*H. axyridis*, 6.0 ± 0.44 individuals/plot, $n = 215$ individuals total; *C. maculata*, 6.3 ± 0.61 individuals/plot, $n = 227$ individuals total), and sample sizes were not significantly different among landscape types for either species (model $F = 1.36$, $df = 23, 48$, $P = 0.18$, $R^2 = 0.40$; full-factor ANOVA for effects of species, habitat abundance and fragmentation).

Movement parameters.—We recorded the individual movement responses of the two coccinellids to landscape structure at four scales: movement within clover cells, movement between clover cells, movement within plots, and movement between plots. Movement rates within clover cells were calculated as the number of clover stems per minute spent in clover cells by each individual. For an analysis of movement between cells, we quantified the rate of movement among clover cells (number of clover cells per minute) and the proportion of cell transitions that were made either by crawling among adjacent cells or by flying (which may or may not have been to an adjacent cell). Additionally, we recorded the cells through which each ladybird beetle moved, which provided a spatial record of its movement pathway across the clover landscape (Wiens et

al. 1993, With 1994). For individuals that made at least five cell transitions, we were able to analyze how landscape pattern affected movement within plots for each species. For each pathway we quantified (1) the mean step length, the mean distance moved from one cell to the next (a step); and (2) the displacement ratio, the net displacement (straight-line distance of the pathway) divided by the overall path length (summation of step lengths) to standardize for differences in the amount of time individuals were observed (displacement ratio of 1.0 is a straight line). Finally, the proportion of individuals that left a plot during the observation period was recorded to obtain a measure of between-plot movement.

Statistical analyses.—Analysis of the effects of landscape pattern on each of these movement parameters (except for proportion leaving plot) involved a full-factor ANOVA (Type III SS) for the main effects of species (*H. axyridis* vs. *C. maculata*), habitat abundance, and fragmentation. Significant differences among means were determined by Tukey hsd tests.

Data for cell movement rates and mean step length were log transformed, and the square root of the proportion of cell transitions made by flying (or crawling) were arcsine transformed (Zar 1999:278), prior to analysis to achieve a normal distribution. Analyses were robust to departures from normality, however, as qualitatively similar results were obtained on the untransformed data. Multiple regression with stepwise selection (P -to-enter = 0.15) was used to assess the relative importance of habitat abundance, degree of fragmentation (clumped or fragmented), mean aphid density (based on the clover cells through which each coccinellid moved), aphid cell occupancy, aphid distribution (Λ), and overall clover distribution (Λ) in explaining movement responses at each of these three scales (movement within cells, between cells and within plots) for each coccinellid species.

Movement among plots was analyzed using chi-square analysis to determine whether the two coccinellids differed in their propensity to leave plots. Logistic regression analysis with stepwise selection (P -to-enter = 0.05) estimated the probability of leaving a plot for each species as a function of the amount of habitat, degree of habitat fragmentation, mean aphid density, aphid cell occupancy, aphid distribution (Λ), and overall clover distribution (Λ).

Search success on experimental fractal landscapes

A relative measure of aphid density was obtained by counting the number of viable pea aphids (excluding parasitized aphids or “mummies”) per 10 clover stems in each cell, averaged across all clover cells through which the focal coccinellid moved. A full-factor ANOVA (Type III ss) tested whether aphid densities differed among cells visited by the two species (species effect) or as a function of landscape structure (effects of habitat abundance and fragmentation).

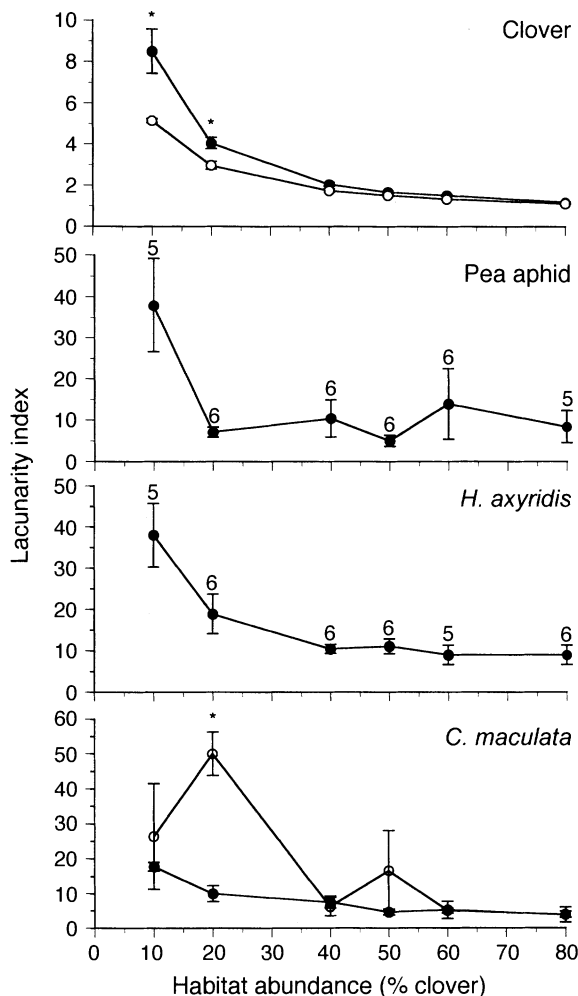


FIG. 2. Species distributional patterns (lacunarity index, Λ) as a function of habitat abundance. Note the change in scale among graphs. Significant differences ($P < 0.05$, Tukey hsd test) between clumped (filled circles) and fragmented (open circles) landscapes at a given level of habitat abundance are indicated by asterisks (*) for clover and *C. maculata* (no significant effects of fragmentation were found for pea aphid or *H. axyridis*, and thus data were pooled). Error bars represent ± 1 SE, and numbers over error bars are sample sizes (all $n = 3$ for clover and *C. maculata*). Pea aphids were not recorded during this survey on one of the 10% fragmented and 80% fragmented plots. *Harmonia axyridis* was not recorded on one of the 10% clumped and 60% clumped plots. Both pea aphids and *H. axyridis* were known to occur on these plots during the first survey period, however.

RESULTS

Effect of landscape structure on species distributions

The distribution of clover in these experimental fractal landscapes exhibited a lacunarity threshold at 20% habitat, indicating that gap sizes (distance among clover patches) become greater and more variable below this level, particularly in clumped landscapes (clover, Fig. 2). In general, the lacunarity index (Λ) was greater for pea aphids and coccinellids than for clover across

TABLE 1. Results of three-way ANOVA (Type III sums of squares) testing the effects of species differences (clover, pea aphid, *Harmonia axyridis*, and *Coleomegilla maculata*), habitat abundance (10%, 20%, 40%, 50%, 60%, and 80% clover) and fragmentation (clumped fractal vs. fragmented fractal distribution of clover) on the lacunarity (scale 2) of species' distributions.

Source of variation	df	MS	F	P
All species (model $R^2 = 0.675$)	47	389.99	4.07	0.0001
Species	3	1394.15	14.54	0.0001
Habitat abundance	5	1307.17	13.63	0.0001
Fragmentation	1	1.88	0.02	0.888
Species \times habitat abundance	15	273.61	2.85	0.001
Species \times fragmentation	3	424.27	4.42	0.006
Habitat abundance \times fragmentation	5	101.53	1.06	0.389
Species \times habitat abundance \times fragmentation	15	150.05	1.56	0.099
Error	92	95.90		
Clover (model $R^2 = 0.954$)	11	14.57	45.16	0.0001
Habitat abundance	5	28.28	87.64	0.0001
Fragmentation	1	6.66	20.63	0.0001
Habitat abundance \times fragmentation	5	2.45	7.60	0.0002
Error	24	0.32		
Pea aphid (model $R^2 = 0.488$)	11	425.35	1.91	0.095
Habitat abundance	5	705.96	3.16	0.027
Fragmentation	1	242.13	1.09	0.309
Habitat abundance \times fragmentation	5	123.70	0.55	0.734
Error	22	223.15		
<i>Harmonia axyridis</i> (model $R^2 = 0.650$)	11	313.82	3.71	0.0043
Habitat abundance	5	611.39	7.24	0.0004
Fragmentation	1	164.43	1.95	0.177
Habitat abundance \times fragmentation	5	58.85	0.70	0.632
Error	22	84.49		
<i>Coleomegilla maculata</i> (model $R^2 = 0.748$)	11	552.72	6.48	0.0001
Habitat abundance	5	674.68	7.91	0.0002
Fragmentation	1	859.66	10.08	0.0041
Habitat abundance \times fragmentation	5	369.36	4.33	0.006
Error	24	85.28		

Note: Because of the significant two-way interactions and marginally significant three-way interaction, separate ANOVAs were performed for each species to test the effects of habitat abundance and fragmentation on the lacunarity of distributions.

all landscapes because insects did not occur in every clover cell, and thus their distribution was more aggregated (greater Λ) than that of their clover habitat. Aphid distributions were significantly related to the distribution of clover ($y = 2.51 + 3.99[\text{clover } \Lambda]$; model $F = 11.46$, $df = 1, 32$, $P = 0.0019$, $R^2 = 0.264$). The distribution of aphids exhibited a strong threshold when clover habitat occupied $<20\%$ of the landscape (pea aphids, Fig. 2; significant effect of habitat abundance, Table 1). Although the lacunarity of clumped landscapes (clover distribution) was significantly greater than that of fragmented landscapes at 10% and 20% habitat ($P < 0.05$, Tukey hsd test), no significant difference in the lacunarity of aphid distributions was found between clumped and fragmented landscapes (Pea aphid, fragmentation effect, Table 1).

The distribution of the biocontrol agent, *H. axyridis*, was also significantly more aggregated when $<20\%$ habitat was present on these landscapes ($P < 0.05$, Tukey hsd test; Fig. 2). This is a weaker threshold response than found in aphids, but like its aphid prey, the distribution of *H. axyridis* was affected by habitat abundance and not by fragmentation (*Harmonia axyridis*, Table 1). The distribution of *H. axyridis* was

strongly related to the distribution of both clover and aphids ($y = 4.62 + 0.25[\text{aphid } \Lambda] + 3.13[\text{clover } \Lambda]$, model $F = 34.87$, $df = 2, 29$, $P = 0.0001$, $R^2 = 0.706$). Most of the variation in the distribution of *H. axyridis* was attributable to the distribution of habitat (clover $R^2 = 64.1\%$) rather than aphids ($R^2 = 6.5\%$), however. Nevertheless, both had a significant effect on the distribution of *H. axyridis* (aphid distribution: $F = 6.42$, $df = 1, 29$, $P = 0.017$; clover distribution: $F = 25.73$, $df = 1, 29$, $P = 0.0001$; two-way ANOVA, Type II SS).

The distribution of the native predator, *C. maculata*, was inversely related to habitat abundance in clumped landscapes (Fig. 2). A threshold response may occur in fragmented landscapes, but at higher levels of habitat ($<40\%$), although the overall response does not coincide with the distribution of clover or aphids. Subsequently, there was a significant habitat abundance \times fragmentation interaction in the distribution of this species (Table 1). The response of *C. maculata* to fragmentation (H) was opposite that of the other species, having a more aggregated distribution in fragmented than in clumped landscapes (Fig. 3). Overall, distributions of *C. maculata* were only weakly related to the

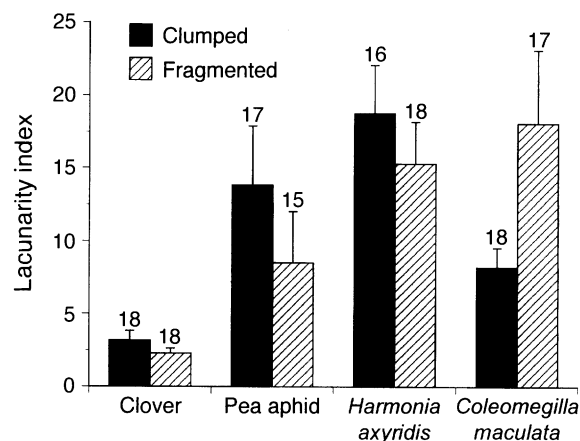


FIG. 3. Species distributional patterns (lacunarity index, Λ) for species in clumped and fragmented fractal landscapes. Error bars represent ± 1 SE. Values above error bars are sample sizes (number of landscape plots).

habitat distribution ($y = 6.82 + 2.49[\text{clover } \Lambda]$, model $F = 4.50$, $df = 1, 32$, $P = 0.042$, $R^2 = 0.123$). Because of the significant effect of fragmentation on *C. maculata* distributions (Table 1), however, we examined the relationship among clover, aphids and *C. maculata* distributions separately in clumped and fragmented landscapes. In clumped landscapes, *C. maculata* exhibited a strong association with the habitat distribution ($y = 2.59 + 1.77[\text{clover } \Lambda]$, model $F = 43.21$, $df = 1, 16$, $P = 0.0001$, $R^2 = 0.730$). The distribution of *C. maculata* was also significantly related to the distribution of clover in fragmented landscapes, but exhibited a negative relationship to the distribution of aphids ($y = -5.88 - 0.846[\text{aphid } \Lambda] + 15.58[\text{clover } \Lambda]$, model $F = 15.25$, $df = 2, 13$, $P = 0.0004$, $R^2 = 0.701$). Of the two, clover had a greater effect on the distribution of *C. maculata* in fragmented landscapes (clover distribution: $F = 30.24$, $df = 1, 13$, $P = 0.0001$, $R^2 = 0.45$; aphid distribution: $F = 10.89$, $df = 1, 13$, $P = 0.0057$, $R^2 = 0.25$).

During the second survey, *H. axyridis* exhibited a more aggregated distribution (higher Λ) than *C. maculata* in these clover landscapes (*H. axyridis*, $56.5 \pm$

9.17Λ ; *C. maculata*, $23.3 \pm 4.06 \Lambda$; significant species effect, Table 2). The higher levels of aggregation attained by both species during the second survey are a result of lower cell occupancy levels relative to the first survey (see *Results: Cell occupancy by coccinellids*). In the absence of pea aphids, *H. axyridis* no longer exhibited a threshold response to landscape structure (compare Fig. 4 to Fig. 2 for *H. axyridis*).

Cell occupancy by coccinellids

During the first survey, species differed significantly in cell occupancy, with pea aphids occurring in 20.8% of clover cells ($\pm 3.04\%$, $n = 33$ plots), *C. maculata* in 17.7% ($\pm 2.38\%$, $n = 36$ plots), and *H. axyridis* in 7.7% of clover cells ($\pm 0.89\%$, $n = 33$ plots; Table 3). Coccinellids were nearly 2.5 times more prevalent on clover landscapes during the first survey than during the second when pea aphids were scarce (proportion of clover cells occupied per landscape, mean ± 1 SE = 0.12 ± 0.014 for survey 1, $n = 69$ species-plot observations [2 species \times 36 plots = 72 observations possible]; 0.05 ± 0.005 for survey 2, $n = 58$; survey effect, Table 4). Species differed in cell occupancy, with the native species, *C. maculata*, occurring in 2.5 times more clover cells than the introduced biocontrol agent, *H. axyridis* (*C. maculata*, 0.12 ± 0.015 , $n = 68$ plot-survey observations; *H. axyridis*, 0.05 ± 0.006 , $n = 59$; significant species effect, Table 4). There was a significant three-way interaction between species, fragmentation, and survey (Table 4). *C. maculata* exhibited higher cell occupancy in clumped landscapes than in fragmented landscapes during the first survey, but no such difference in patch occupancy occurred during the second survey when pea aphids were absent (Fig. 5).

Relative effects of landscape structure and aphid distributions on predator search behavior

The two coccinellids differed significantly in all aspects of movement behavior (significant species effect, Table 5). The native predator, *C. maculata*, exhibited more active search behavior than *H. axyridis* within clover cells, moving significantly more among clover stems (Table 6). However, *H. axyridis* was more likely

TABLE 2. Results of three-way ANOVA (Type III sums of squares) testing the effects of species (*Coleomegilla maculata* and *Harmonia axyridis*), habitat abundance, and fragmentation of the lacunarity (scale 2) of species' distributions in the absence of aphids (second survey).

Source of variation	df	MS	F	P
Model ($R^2 = 0.420$)	22	1571.24	1.12	0.375
Species	1	12049.12	8.59	0.006
Habitat abundance	5	639.00	0.46	0.806
Fragmentation	1	695.50	0.50	0.486
Species \times habitat abundance	5	1388.98	0.99	0.438
Species \times fragmentation	1	3960.50	2.82	0.102
Habitat abundance \times fragmentation	5	487.38	0.35	0.880
Species \times habitat abundance \times fragmentation	4	735.51	0.52	0.719
Error	34	1403.31		

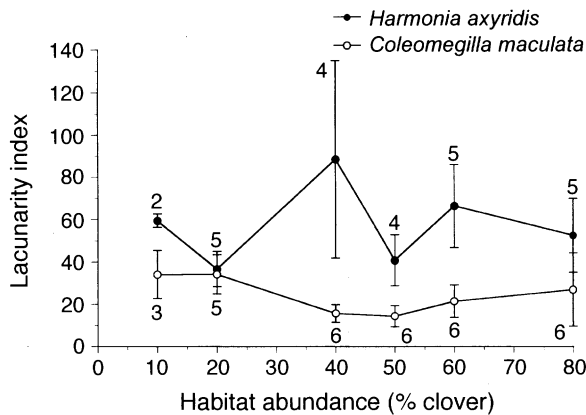


FIG. 4. Distributional patterns (lacunarity index, Λ) of two coccinellids (*Harmonia axyridis* and *Coleomegilla maculata*) as a function of habitat abundance in the absence of pea aphids. Error bars represent ± 1 SE, and numbers above or below error bars are sample sizes (number of landscape plots).

to move between clover cells and plots because it tended to fly more than *C. maculata* (Table 6). As a consequence, *H. axyridis* moved twice as far and twice as fast between cells for an overall displacement ratio that was 2.6 times greater than that of *C. maculata* within plots, and was three times more likely to move between plots than *C. maculata* (species effect: $\chi^2 = 25.07$, $df = 1$, $P < 0.0001$; Table 6).

The effect of landscape structure on search behavior was apparent in the significant effect of fragmentation on the rate of movement between clover cells and by the effect of habitat abundance on displacement within plots (Table 5). In general, coccinellids (both species combined) moved faster among clover cells when in fragmented landscapes (clumped, 0.13 ± 0.009 clover cells/min in clover; fragmented, 0.19 ± 0.072 clover cells/min in clover) and moved four times farther in 50% landscapes than in landscapes that had only 10% or 20% clover (Fig. 6a).

The proportion of clover cells occupied by aphids (aphid cell occupancy) significantly affected the probability that *H. axyridis* would leave the plot during observations ($\text{logit}[\text{probability left plot}] = -0.41 -$

$3.47[\text{aphid cell occupancy}]$; parameter Wald $\chi^2 = 8.45$, $P = 0.0036$). No factor significantly affected whether *C. maculata* would leave, perhaps because so few individuals were observed to move between plots (22 out of 227 observations). Although the odds that *H. axyridis* would leave a plot during observations were small (0.031), plots that *H. axyridis* left had lower occupancy by aphids (mean ± 1 SD = 0.11 ± 0.129 , $n = 62$ observations) than those where they stayed (0.18 ± 0.174 , $n = 153$ observations). Movement pathways of *H. axyridis* became significantly more tortuous (displacement ratio approaches 0) as aphid cell occupancy on landscapes increased ($y = 0.95 - 0.78[\text{aphid cell occupancy}]$, $F = 7.20$, $df = 1, 21$, $P = 0.0139$, $R^2 = 0.25$; Fig. 6b). Aphid density or distribution (Λ) explained little of the variation in movement rates within or between cells for *H. axyridis* ($R^2 < 0.10$), and had no significant effect on the rate of movement at either of these scales for *C. maculata*.

Search success on experimental fractal landscapes

Mean pea aphid densities within clover cells were slightly higher on clumped landscapes than in fragmented clover landscapes (clumped, 2.1 ± 0.19 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; fragmented, 1.7 ± 0.18 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; significant fragmentation effect, Table 7). Overall, *H. axyridis* foraged in clover cells that had a higher density of pea aphids than those visited by *C. maculata* (*H. axyridis*, 0.61 ± 0.084 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; *C. maculata*, 0.45 ± 0.072 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; significant species effect, Table 7). There was a significant species \times fragmentation interaction, however, such that it was only in clumped landscapes that *H. axyridis* was apparently able to maximize its search success and foraged in cells with significantly higher pea aphid densities than those visited by *C. maculata* (*C. maculata*, clumped, 1.61 ± 0.198 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; fragmented, 1.69 ± 0.267 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; *H. axyridis*, clumped, 2.72 ± 0.336 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; fragmented, 1.74 ± 0.237 aphids $\cdot [10 \text{ stems}]^{-1} \cdot [\text{clover cell}]^{-1}$; Table 7). This difference between species in search success on clumped landscapes was especially pronounced when clover hab-

TABLE 3. ANOVA summary (Type III sums of squares) of how cell occupancy varies among species (pea aphid, *Coleomegilla maculata*, and *Harmonia axyridis*) and as a function of landscape structure (habitat abundance and fragmentation).

Source of variation	df	MS	F	P
Model ($R^2 = 0.442$)	35	0.05	1.50	0.079
Species	2	0.27	8.81	0.0004
Habitat abundance	5	0.03	0.87	0.503
Fragmentation	1	0.00	0.06	0.806
Species \times habitat abundance	10	0.04	1.17	0.329
Species \times fragmentation	2	0.13	4.21	0.019
Habitat abundance \times fragmentation	5	0.00	0.11	0.990
Species \times habitat abundance \times fragmentation	10	0.02	0.78	0.645
Error	66	0.03		

TABLE 4. Comparison of cell occupancy between surveys (pea aphids present vs. pea aphids absent) for two coccinellids (*Coleomegilla maculata* and *Harmonia axyridis*) as a function of landscape structure (habitat abundance and fragmentation) based on a full-factorial ANOVA (Type III sums of squares).

Source of variation	df	MS	F	P
Model ($R^2 = 0.619$)	46	0.04	2.82	0.0001
Survey	1	0.51	35.23	0.0001
Species	1	0.36	24.62	0.0001
Habitat abundance	5	0.04	2.47	0.039
Fragmentation	1	0.02	1.21	0.276
Survey \times species	1	0.02	1.14	0.289
Survey \times habitat abundance	5	0.01	0.46	0.808
Survey \times fragmentation	1	0.02	1.07	0.305
Species \times habitat abundance	5	0.02	1.29	0.277
Species \times fragmentation	1	0.01	0.75	0.389
Habitat abundance \times fragmentation	5	0.01	0.38	0.859
Survey \times species \times habitat abundance	5	0.02	1.10	0.366
Survey \times species \times fragmentation	1	0.08	5.49	0.022
Species \times habitat abundance \times fragmentation	5	0.01	0.58	0.718
Survey \times species \times abundance \times fragmentation	9	0.01	0.98	0.460
Error	80	0.01		

it was rare (10–20%); *H. axyridis* foraged in clover cells that had nearly 2.5 to 3.5 times more pea aphids than those cells visited by *C. maculata* (significant three-way interaction, Table 7; Fig. 7).

DISCUSSION

The effective scale of biological control

Does the successful control of insect pests ultimately depend upon the search success of individual predators, the ability of predators to aggregate within patches in response to local prey density, or the ability of predators to aggregate at the “landscape scale” in response to the distribution of prey populations? In other words, at what scale(s) does biocontrol effectively occur? This is an important question, especially if habitat fragmentation compromises biocontrol efforts by interfering with predator search behaviors and disrupts predator–prey interactions by affecting the ability of predators to aggregate in response to prey density or to track prey distributions. The first step in evaluating the effective scale of biological control thus lies in determining how predator search behaviors are affected by the scale of fragmentation.

Species that vary in mobility or dispersal ability are expected to vary in their response to fragmentation and will have different perceptions as to whether the landscape is in fact fragmented (Doak et al. 1992, With and Crist 1995, Pearson et al. 1996). The assumption that habitat fragmentation interferes with predator search success and prevents aggregation in areas of high prey density—whether within individual habitat patches or among patches (prey metapopulations) across a landscape (Kareiva 1987, Roland and Taylor 1997)—implies that the individual movement responses of predators are translated across scales and affect population-level phenomena such as predator–prey interactions (e.g., Turchin 1989, 1991, With and Crist 1996). Can we predict the strength of such interactions from the

finer scale responses of individuals' to heterogeneity, however? Maybe. Different patterns may emerge at different scales, and the aggregate response may be stronger than the individual response. For example, Ives et al. (1993) found that the amount of time individual ladybird beetles (*Coccinella septempunctata* and *Hippodamia variegata*) spent on fireweed stems was only

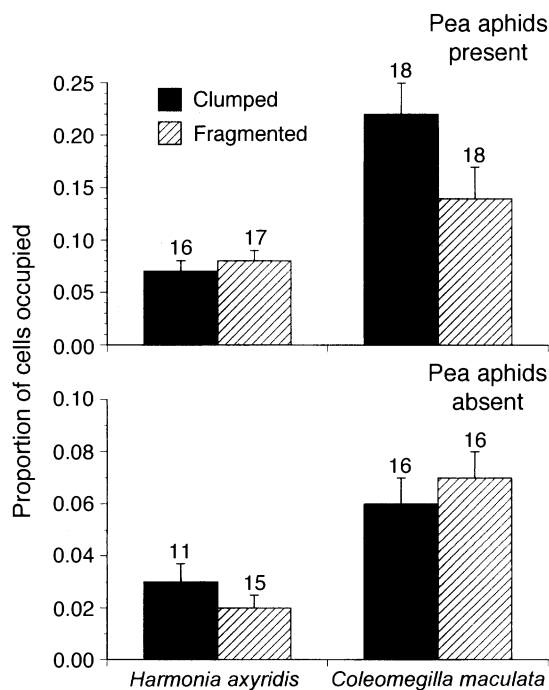


FIG. 5. Clover cell occupancy by two coccinellids (*Harmonia axyridis* and *Coleomegilla maculata*) in clumped and fragmented landscapes when aphids are present (first survey, 1–14 June 1998) and when they are absent (second survey, 28 June–12 July 1998). Error bars represent ± 1 SE, and numbers above error bars are sample sizes (number of landscape plots).

TABLE 5. Results of three-way ANOVA (Type III sums of squares) testing the effects of species (*Coleomegilla maculata* vs. *Harmonia axyridis*), habitat abundance, and fragmentation on various attributes of movement for these two coccinellids in experimental clover landscapes.

Source of variation	df	MS	F	P
Within cells				
Clover stem movement rate (stems/min clover; model $R^2 = 0.104$)	23	1.09	1.55	0.053
Species	1	11.07	15.69	0.0001
Habitat abundance	5	0.20	0.28	0.926
Fragmentation	1	0.01	0.01	0.928
Species \times habitat abundance	5	0.41	0.58	0.718
Species \times fragmentation	1	0.16	0.22	0.639
Habitat abundance \times fragmentation	5	1.21	1.72	0.129
Species \times habitat abundance \times fragmentation	5	0.60	0.85	0.514
Error	309	0.71		
Between Cells				
Clover cell movement rate (clover cells/min clover \ddagger ; model $R^2 = 0.074$)	23	1.28	1.44	0.088
Species	1	6.10	6.87	0.009
Habitat abundance	5	1.56	1.76	0.120
Fragmentation	1	4.01	4.51	0.034
Species \times habitat abundance	5	1.05	1.18	0.318
Species \times fragmentation	1	0.32	0.36	0.548
Habitat abundance \times fragmentation	5	1.04	1.17	0.325
Species \times habitat abundance \times fragmentation	5	0.39	0.44	0.823
Error	415	0.89		
Proportion of cell transitions by flight \ddagger ; model $R^2 = 0.399$	22	1.52	4.32	0.0001
Species	1	15.96	45.46	0.0001
Habitat abundance	5	0.37	1.04	0.395
Fragmentation	1	0.74	2.10	0.149
Species \times habitat abundance	5	0.16	0.47	0.799
Species \times fragmentation	1	0.08	0.21	0.644
Habitat abundance \times fragmentation	5	0.29	0.82	0.540
Species \times habitat abundance \times fragmentation	5	0.18	0.51	0.732
Error	143	0.35		
Within Plot				
Mean step length (m \ddagger ; model $R^2 = 0.392$)	20	0.21	1.39	0.181
Species	1	1.06	7.12	0.011
Habitat abundance	5	0.19	1.29	0.285
Fragmentation	1	0.00	0.00	0.996
Species \times habitat abundance	4	0.03	0.18	0.948
Species \times fragmentation	1	0.01	0.09	0.762
Habitat abundance \times fragmentation	4	0.02	0.16	0.955
Species \times habitat abundance \times fragmentation	3	0.02	0.11	0.953
Error	43	0.15		
Displacement ratio (net displacement/path length; model $R^2 = 0.566$)	20	0.13	2.80	0.0023
Species	1	0.89	19.01	0.0001
Habitat abundance	5	0.14	3.05	0.019
Fragmentation	1	0.01	0.13	0.720
Species \times habitat abundance	4	0.04	0.78	0.542
Species \times fragmentation	1	0.00	0.00	0.974
Habitat abundance \times fragmentation	4	0.05	0.99	0.425
Species \times habitat abundance \times fragmentation	3	0.02	0.40	0.755
Error	43	0.05		

\ddagger Data were log transformed prior to analyses.

\ddagger The square root of each proportion was arcsine transformed prior to analysis.

weakly correlated with aphid density. This might lead one to predict that these two coccinellids would not be particularly effective in controlling aphid outbreaks, a surprising result given that both were introduced specifically as biocontrol agents of aphids (Gordon and Vandenberg 1991, Obrycki and Kring 1998). Despite the apparent inefficiency of individual ladybird beetles, however, populations of ladybird beetles exhibited a strong correlation with the number and size of aphid populations within plots. Thus, the aggregate response of individuals at a broader scale effectively averaged out the variation observed at the finer scale of indi-

vidual responses to aphid densities (Ives et al. 1993). Similarly, in our study, *C. maculata* moved most rapidly among clover stems, which should enhance its ability to locate aphids. Given its tendency to crawl among clover stems, however, fine-scale habitat connectivity provided by overlapping clover stems or leaves is ultimately required for effective search and aggregation. This is corroborated by the observation by Kareiva and Perry (1989) that the degree of leaf overlap substantially altered movement rates and trajectories in *Hippodamia convergens*, behaviors which have been shown to affect search success in coccinel-

TABLE 6. Search behavior of two ladybird beetles, *Harmonia axyridis* and *Coleomegilla maculata*, at different scales within experimental clover landscapes (see Fig. 1).

Scale and behavior measure	<i>H. axyridis</i>	<i>C. maculata</i>
Within Cells		
Clover stems (stems/clover min)	0.8 ± 0.05 (151)	1.2 ± 0.07 (182)
Between Cells		
Clover cells (cells/clover min)	0.22 ± 0.071 (214)	0.10 ± 0.007 (225)
Primary mode of movement	fly	crawl
Proportion of cell transitions in this mode	0.793 ± 0.04 (76)	0.728 ± 0.04 (90)
Within Plot		
Mean step length (m)	1.9 ± 0.21 (29)	1.1 ± 0.04 (35)
Displacement ratio (net displacement/path length)	0.49 ± 0.051 (29)	0.19 ± 0.030 (35)
Between Plots		
Proportion leaving plot (during observation period)	0.288 (215)	0.097 (227)

Note: Values are means ± 1 SE with sample sizes (number of individuals) in parentheses.

lids (Kareiva and Odell 1987). Thus, *C. maculata* operates at a finer spatial scale than *H. axyridis* and is particularly sensitive to the scale of fragmentation in these clover landscapes, which ultimately may have prevented it from tracking aphid distributions in fragmented landscapes. This is supported by the negative association that we found between *C. maculata* and aphid distributions on fragmented landscapes. The results of our study for *C. maculata* are thus in general agreement with Kareiva's (1987) classic study of fragmentation effects on predator-prey interactions, in which *Coccinella septempunctata* was able to aggregate more rapidly to aphid clusters in continuous goldenrod habitat than in fragmented habitat, presumably because fragmentation interfered with their search behavior.

Kareiva cautioned against making generalizations regarding the effects of fragmentation on predator-prey interactions, however, given that the effects of habitat fragmentation depend upon the specifics of the species' dispersal behavior and demography. Given its greater mobility, *H. axyridis* operates at a broader spatial scale and thus should be more effective at tracking the spatiotemporal dynamics of aphids in this system, owing to its greater tendency to fly among clover cells and landscapes. Such efficacy in locating and controlling pest populations when they occur at low densities or cell occupancy (e.g., aphids in landscapes with <20% clover) is obviously a requisite for successful biocontrol. Nevertheless, it was only in clumped landscapes with 10–20% clover that *H. axyridis* was significantly more successful than *C. maculata*, foraging in clover cells with 2.5–3 times more aphids. Given that coccinellids are apparently not able to detect aphids over long distances (e.g., Nakamuta 1984), it is likely that the greater search success of *H. axyridis* was not due to selective foraging, but to a more rapid and broad-scale search behavior that resulted in an increased encounter rate with clover cells that contained higher aphid densities. Once encountered, *H. axyridis* may spend more time in clover cells with aphids, and more time in landscapes with greater aphid occupancy, which is suggested by the more

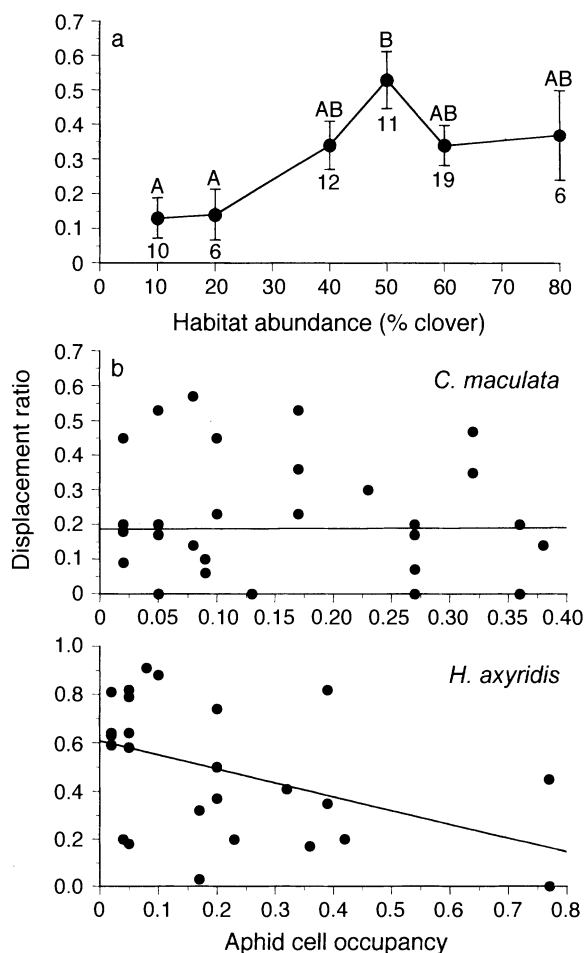


FIG. 6. (a) Displacement ratio of coccinellid movement pathways (combined data for *Harmonia axyridis* and *Coleomegilla maculata*) searching in landscapes that differed in amount of clover habitat. Error bars represent ± 1 SE, numbers below bars are sample sizes (number of ladybird beetles observed), and points with the same letter are not significantly different ($P > 0.05$, Tukey hsd). (b) Relationship between the displacement ratio and aphid cell occupancy (proportion of clover cells occupied by aphids on a landscape plot) for the two coccinellids. Lines are fitted by linear regression.

TABLE 7. Results of a three-way ANOVA (Type III sums of squares) to assess how search success (number of aphids·[10 stems]⁻¹·[clover cells visited by each coccinellid individual]⁻¹) varied between the two coccinellids (*Coleomegilla maculata* vs. *Harmonia axyridis*) as a function of habitat abundance and fragmentation in experimental clover landscapes.

Source of variation	df	MS	F	P
Model ($R^2 = 0.091$)	23	12.50	1.79	0.015
Species	1	34.26	4.90	0.027
Habitat abundance	5	5.17	0.74	0.593
Fragmentation	1	50.91	7.29	0.007
Species × habitat abundance	5	8.04	1.15	0.333
Species × fragmentation	1	19.51	2.79	0.095
Habitat abundance × fragmentation	5	7.24	1.04	0.396
Species × habitat abundance × fragmentation	5	18.01	2.58	0.026
Error	411	6.98		
<i>C. maculata</i> (model $R^2 = 0.117$)	11	13.44	2.53	0.0051
Habitat abundance	5	10.39	1.96	0.086
Fragmentation	1	3.64	0.69	0.409
Habitat abundance × fragmentation	5	19.89	3.75	0.003
Error	210	5.31		
<i>H. axyridis</i> (model $R^2 = 0.058$)	11	9.80	1.12	0.346
Habitat abundance	5	3.75	0.43	0.828
Fragmentation	1	67.74	7.75	0.006
Habitat abundance × fragmentation	5	6.35	0.73	0.604
Error	201	8.74		

Note: Because of the significant three-way interaction, separate analyses were also performed for each species.

tortuous movement pathways exhibited on these landscapes (i.e., displacement ratio approaches 0). Collectively, these movement responses may account for the congruence in the lacunarity of *H. axyridis* distributions with that of clover and pea aphids.

Is the ability to aggregate at a broader scale (the "landscape scale") and track the distribution of prey populations the key to successful biological control, then? The most compelling finding of our study was that thresholds in landscape structure can be perpetuated across trophic levels, producing similar thresholds in the distribution of pest populations. Are natural enemies primarily responding to thresholds in landscape structure or thresholds in prey distributions? Given that insect herbivores may themselves reflect thresholds in the distribution of their host plant (this study), the direct and indirect effects of landscape thresholds on bio-control may be hard to separate. In this system, however, it appears that the distribution of *H. axyridis* is more closely tied to the distribution of clover than aphids. Successful biological control may rest on the ability of natural enemies to track thresholds in prey distributions, which in turn is a consequence of how the scale of fragmentation affects the movement response or search success of natural enemies in landscapes below the threshold. This, then, provides a mechanistic link between individual movement responses and population-level phenomena that affect predator-prey interactions in fragmented landscapes.

Implications for conservation biological control

Ideally, agricultural systems could be designed or managed to preserve habitat connectivity and thus enhance the efficiency of natural enemies (Kruess and Tscharrntke 1994), which is the goal of the emerging

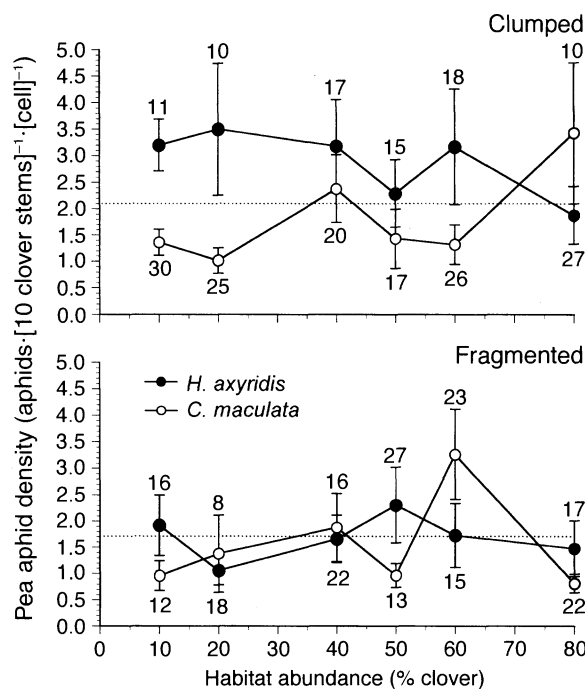


FIG. 7. Pea aphid densities (number of aphids·[10 stems]⁻¹·[clover cell]⁻¹) within cells visited by two coccinellids (*Harmonia axyridis* and *Coleomegilla maculata*) in clumped and fragmented clover landscapes. Dashed horizontal lines represent the mean aphid cell density across all landscapes of a given type (clumped or fragmented). Error bars represent ± 1 SE, and numbers above or below error bars are sample sizes (number of ladybird beetles).

discipline of conservation biological control (Barbosa 1998). Much of the focus in conservation biological control has centered on increasing habitat diversity or cropping systems within these managed landscapes, however, rather than on spatial considerations related to minimizing fragmentation effects (Gurr et al. 1998). The existence of thresholds in landscape structure has important implications for the biological control of insect pests. Although the success of biocontrol is usually assessed in terms of the ability of natural enemies to maintain pest populations below economic thresholds of damage, there are also ecological thresholds that must be surmounted if biocontrol measures are to be successful. Biocontrol is most successful when prey are unable to find refuge from natural enemies (Hawkins et al. 1993). Because thresholds in landscape structure can disrupt the search efficiency and aggregative response of natural enemies, pest populations might build up in "refuges" afforded by isolated habitat fragments on those landscapes lying below the threshold (e.g., <20% habitat), spread to other landscapes that are not infested, and thus increase the potential for pest outbreaks across a broader region.

Although we discovered that such thresholds in the aggregative response of predators occurred in landscapes with <20% habitat, this must not be embraced as a general management guideline as to the total amount of a particular habitat or crop type that should be preserved on the landscape. If anything, this should only be viewed as a minimum amount of habitat that must be maintained to avoid disrupting predator foraging behavior or search success, which says nothing about whether there is sufficient habitat to support viable populations of these predators or a diverse assemblage of natural enemies that would enhance biocontrol efforts. Different habitat threshold values emerge depending upon whether the effects of landscape structure on search behavior, distributional patterns, population persistence, predator-prey interactions, or communities are being assessed (Lande 1987, Tilman et al. 1994, Kareiva and Wennergren 1995, With and Crist 1995, Bascompte and Solé 1996, 1998, With and King 1999a, b).

The future of biological control in fragmented landscapes

Our study raises an additional question about whether indigenous insect predators or parasitoids are generally more sensitive to the effects of fragmentation than exotic species. Obviously, a species like *H. axyridis* that was introduced specifically for the purposes of biological control should have the desired traits of high mobility and search efficiency (Murdoch and Briggs 1996). Such traits may have the added advantage of enabling these introduced biocontrol agents to operate effectively in fragmented landscapes and to overcome thresholds in landscape structure to track and regulate pest populations. Nevertheless, if exotic species are generally more mobile than native species and

if this mobility makes them more amenable as biocontrol agents, then this raises the concern that we will become increasingly dependent upon the introduction of exotic species to control pest outbreaks as agroecosystems and other managed landscapes continue to be fragmented. This is obviously not without economic costs and ecological risks to the native insect community (Simberloff and Stiling 1996). The adverse ecological effects of habitat fragmentation and exotic biocontrol agents may thus compromise conservation biological control programs that strive to manipulate the environment in ways to augment indigenous populations of natural enemies. Affording a diversity of habitat types or refugia for natural enemies may not be sufficient unless the threshold effects of landscape structure are also mitigated.

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