DIFFERENTIAL RESPONSE OF TWO AGROECOSYSTEM PREDATORS, *PTEROSTICHUS MELANARIUS* (COLEOPTERA: CARABIDAE) AND *COCCINELLA SEPTEMPUNCTATA* (COLEOPTERA: COCCINELLIDAE), TO HABITAT-COMPOSITION AND FRAGMENTATION-SCALE MANIPULATIONS

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Abstract

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Using alternating patches of weeds and crop [broccoli, *Brassica oleracea* (L.) (Brassicaceae)], vegetation composition and the spatial scale at which the vegetation was fragmented were manipulated in a factorial design field experiment. The effects of these manipulations were different for two common agroecosystem predators sampled. Sevenspotted lady beetles, *Coccinella septempunctata* (L.), were unaffected by vegetation-composition treatments but responded strongly to fragmentation-scale manipulations. The beetle *Pterostichus melanarius* (Illiger) was unaffected by both fragmentation-scale and vegetation-composition manipulations. These findings highlight the challenge of developing a predictive theory of the effects of vegetation diversification on assemblages of predators in agroecosystems.

Banks JE 1999. Réponses différentes de deux prédateurs d'un agro-écosystème, *Pterostichus melanarius* (Coleoptera: Carabidae) et *Coccinella septempunctata* (Coleoptera: Coccinellidae), aux manipulations de la composition de l'habitat et de l'échelle de fragmentation. *The Canadian Entomologist* **131**: 645 – 657.

Résumé

Lors d'une expérimentation dans les plantations utilisant la méthode factorielle, j'ai manipulé la composition de la végétation de même que l'échelle spatiale à laquelle la végétation a été fragmentée en utilisant alternativement des zones de broccoli [*Brassica oleracea* (L.) (Brassicaceae)] et de mauvaises herbes. Les effets de ces manipulations se sont avérés différents pour les deux prédateurs communs échantillonés dans l'agro-écosystème. La coccinelle à sept points, *Coccinella septempunctata* (L.), s'est montrée insensible aux traitements de la composition, mais a réagi fortement aux manipulations de l'échelle de fragmentation. La carabe *Pterostichus melanarius* (Illiger) s'est montrée indifférent aux manipulations de la composition de la végétation ainsi qu'à celles de l'échelle de fragmentation. Ces résultats soulignent les difficultés inhérentes au développement d'une théorie prophétique des effets de la diversité de la végétation sur les asssociations des prédateurs dans les agro-écosystèmes.

Introduction

In the past two decades, ecologists have put much effort into understanding how habitat heterogeneity affects insect populations in agroecosystems. One widely cited route by which landscape or vegetation pattern can influence insect populations is Root's (1973) hypothesis that more diverse landscapes tend to harbor more abundant and diverse predators, and thus facilitate better control of pest populations than homogeneous landscapes. Some empirical evidence supports this hypothesis, typically documenting either reduced pest populations (Andow 1983, 1991) or increased predator

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abundance (Letourneau and Altieri 1983; Letourneau 1987) in more diverse systems. Furthermore, recently there has been renewed focus in biological control research on bolstering natural enemy populations *via* habitat diversification (Gross 1987; Chiverton and Sotherton 1991; Dennis and Fry 1992; Tonhasca 1993; Colunga-Garcia *et al.* 1997).

Reviews of experiments aimed at understanding the effects of increased vegetation diversity on insect populations, however, suggest that increased vegetation diversity has at most only moderate effects on insect populations (Tonhasca and Byrne 1994). In particular, experimental increases in vegetation diversity have resulted variously in increases, decreases, or no changes in population abundances of both pests and predators (Risch *et al.* 1983; Sheehan 1986; Russell 1989; Andow 1991), underscoring how difficult it is to make generalizations about the effects of habitat diversity on agroecosystem insect populations.

One factor that is often overlooked in attempts to generalize about the effects of vegetation diversity is that insects within a given agroecosystem span a range of dispersal abilities. Because dispersal characteristics are important in determining the outcome of predator–prey interactions (Gause 1934; Huffaker 1958; Luckinbill 1973; Kareiva 1987; Corbett and Plant 1993), it follows that insects with differing dispersal abilities might be differentially affected by vegetation diversification. Furthermore, the scale at which vegetation diversity is deployed may interact with insects' dispersal abilities to create further differences in the way different insects respond to vegetation diversification. There have been many experiments that examine the impact that vegetation pattern has on natural enemies (Landis and Haas 1992; Kruess and Tscharntke 1994; Russell 1989), but few have explicitly addressed the consequences of the scale at which the patterning is expressed on predators with differing dispersal abilities (but see Marino and Landis 1996; and Roland and Taylor 1997 for parasitoid examples).

I report on manipulative field experiments designed to assess whether vegetation composition and the scale at which vegetation is fragmented have a significant impact on the distributions of two common agricultural predators with contrasting dispersal behaviors. I assessed this impact by establishing plots with mixtures of broccoli, *Brassica oleracea* (L.) (Brassicaceae), and weed patches in different proportions and at different scales of fragmentation.

Materials and Methods

Experimental System. The experimental system consisted of mixtures of the common crucifer broccoli and natural weedy vegetation. In the western part of the State of Washington, broccoli attracts several insect herbivores, including the cabbage aphid, *Brevicoryne brassicae* (L.), green peach aphid, *Myzus persicae* (Sulzer), and turnip aphid, *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae). These pests attract several predators, the most prevalent of which are *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) and *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae). Carabids are mandibulate generalist predators common in agricultural areas; most are nocturnal, surface-dwelling foragers feeding on aphids, lepidopteran larvae, spiders, beetles, and other arthropods (Lovei and Sunderland 1996). Carabids will climb up onto foliage to prey on aphids and other insects and feed on arthropods that become disturbed by predators or parasitoids and fall off plant surfaces onto the ground (Losey and Denno 1998*a*). *Pterostichus melanarius*, an exotic species thought to have been introduced from Europe to North America in ship ballast in the early part of this century (Lindroth 1957), was the most abundant carabid in my experimental plots.

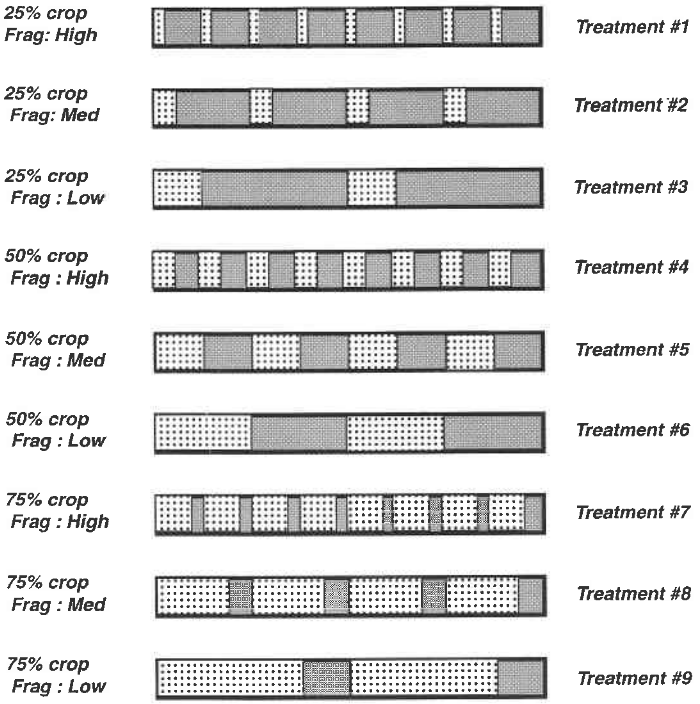

Figure 1. Schematic of all nine treatment arrays. Dotted areas represent patches of *Brassica oleracea*, and shaded areas denote weeds (see text for list of species). Notation next to each strip indicates the percentage of array consisting of broccoli. Frag, fragmentation scale.

Ladybird beetles are voracious predators, feeding primarily on aphids, though they will consume other insects and pollen (Hagen 1962). The most common species in the experimental plots, *C. septempunctata*, was introduced to the United States in the 1950s (Angalet *et al.* 1979). Establishing in the 1970s, it was ubiquitous in the United States by the 1980s and has since become so successful that there is concern that it has begun displacing some native coccinellid communities (Elliott *et al.* 1996; Obrycki *et al.* 1998). *Coccinella septempunctata* typically flies among plants or patches of plants, then walks around the foliage of individual plants searching for prey.

Experimental Design. This study was designed to assess the effects of two aspects of vegetation diversity on these two predators: (1) plant composition, manipulated by establishing plots in which the proportion of broccoli plants and weedy vegetation varied; and (2) the scale of vegetation fragmentation, manipulated by varying the scale at which broccoli and weed patches were fragmented.

The experimental design was a two-way factorial balanced design in which three levels of plant composition, measured as proportion of plots consisting of broccoli, were crossed with three scales of fragmentation, recorded as a measure of how broccoli and weed patches were broken up in experimental plots. Experimental plots were long rectangular arrays, 2 m wide and 32 m long, in which patches of broccoli and naturally occurring weeds were grown in various combinations (Fig. 1). Each array represented one treatment combination of vegetation diversity (percent crop cover) and fragmentation scale, with composition levels consisting of either 25, 50, or 75% broccoli crop cover, each at low, medium, or high levels (scale) of fragmentation. In all cases, regardless of percent crop cover, low fragmentation meant that the total combined length (lengthwise along the array) of one crop patch plus one weed patch equaled 16 m; total length of one crop patch plus one weed patch was 8 m and 4 m for all medium and high fragmentation scale treatments, respectively. The total experiment consisted of three replicates of the total factorial design for a total of 27 arrays, all planted on approximately 1 ha of land at the Washington State University Research and Extension Center's Farm Two in Puyallup, Washington. All 27 experimental arrays (*i.e.*, all three replicates) were established in both the 1994 and the 1995 growing seasons. Arrays were randomly arranged within each block (replicate), with rearrangement each year. Within each array, broccoli areas consisted of two rows of broccoli plants separated by 1 m; the broccoli plants within each row were spaced at 50-cm intervals. All but seven of the arrays were laid out parallel to one another, separated by 3 m of bare ground on either side. Because of spatial constraints, the remaining seven arrays were laid out perpendicular to the other 20 arrays; they were separated from the ends of the other arrays by at least 5 m, and were themselves surrounded on either side by 3 m of bare ground. The area around plants in broccoli patches was kept cultivated by weekly hand hoeing; the bare ground between experimental arrays was kept free of vegetation by regular plowing with a tractor.

Long rectangular plots were used as a reasonable approximation to the cost-prohibitive alternative, the deployment of 27 different full-sized fields, for measuring predator responses to the vegetation-diversity manipulations. Furthermore, focusing on predator distributions along "two-dimensional" swaths of vegetation enabled me to simplify the interpretation of the resulting predator density patterns. Linear array shaped plots surrounded by bare ground or minimal ground cover have been used successfully in the past to quantify beetle (including coccinellid) responses to vegetation texture and patchiness (Kareiva 1987). Regular plowing in between arrays in the current experiment created a regular physical disturbance to the vertical and horizontal soil biota, representing a qualitative barrier to movement for most insects that stood in contrast to the minor disturbances (*i.e.*, hand-hoeing) within arrays (Stinner and House 1990). To measure the degree to which predators might have moved across bare ground alleys to adjacent arrays, an analysis designed to quantify the influence of neighboring arrays on predator densities in each array was performed (see Statistical Analyses). This test was performed to better interpret distributions of predators arising from the vegetation manipulations.

All arrays were irrigated regularly and as uniformly as possible. Broccoli plants were grown from seed in a greenhouse on the University of Washington campus, then planted into the field during the first week of June in 1994 and the second week of June in 1995. In non-broccoli areas within arrays, weeds were allowed to colonize and to grow naturally. The weedy vegetation in the experimental arrays was dominated by *Echinochloa colonum* (L.) (Poaceae), *Echinochloa crusgalli* (L.) (Poaceae), *Cirsium arvense* (L.) (Asteraceae), *Chenopodium album* (L.) (Chenopodiaceae), *Polygonum lapathifolium* (L.) (Polygonaceae), *Amaranthus powellii* S. Watson (Amaranthaceae), *Equisetum arvense* (L.) (Equisetaceae), *Sonchus asper* (L.) (Asteraceae), and *Lamium amplexicaule* (L.) (Lamiaceae).

Predator Sampling. Carabids were collected in pitfall cup traps set into the ground at 2-m intervals in the middle of each treatment array along the length of each array (16 cups per array). This spacing was established to ensure sampling of beetles occurred in both broccoli and weed patches in all treatment arrays (with an average ± SE of 8.04 ± 2.76 pitfalls in the crop areas of each array), and also to minimize bias due to sampling from the edges of arrays. Although pitfall traps would likely yield more independent samples if they were spaced farther apart (Digweed *et al.* 1995), traps were spaced to accommodate the lowest fragmentation treatment and then spaced at the same distance for all treatment arrays to avoid biases due to variation in sampling spatial scale (Spence and Niemelä 1994). For each carabid sample date during the growing season, I set traps in the evening, and collected, recorded, and rereleased specimens the following morning into the arrays from which they had been caught.

Because *C. septempunctata* is adept at flight, I visually counted individuals in arrays in timed passes through both broccoli and weedy vegetation. I spent 4 min walking the length of each treatment array, tallying the number of beetles in both broccoli and weed patches, without disturbing or removing any individuals. I paced my progress through each array such that the vegetation in each 8-m section was examined for 1 min (8 m × 4 = 32 m) to keep sampling effort equal in all sections of all treatments; this was ample time to thoroughly examine all of the vegetation in either broccoli or weed patches. Because coccinellid activity is sensitive to weather conditions, I avoided sampling on especially cold or rainy days during the growing season.

Each predator was sampled a total of five times across the two growing seasons. The carabid was sampled three times in 1994 (20 July, 9 August, and 15 August) and twice in 1995 (21 July and 5 August); the coccinellid was sampled three times in 1994 (24 July, 5 August, and 26 August) and twice in 1995 (25 July and 18 August).

Statistical Analyses. Overall average densities for each treatment were compared with a MANOVA, with the five sample dates as the multiple variables (Wilkinson 1992; Scheiner 1993; von Ende 1993). I tested for overall responses of each predator to percent crop cover and fragmentation manipulations. I analyzed means from treatments from all five sample dates together because some correlation between the two growing seasons, due to probable overwintering of predators in nearby areas, could not be ruled out. To obtain more information about the nature of differences in density responses to different treatments, in cases identified as significant by the MANOVA, I plotted predator densities averaged over all sample dates for particular treatment effects. Furthermore, for both carabid and coccinellid counts I also noted whether predators recorded in treatment arrays were found in crop areas or weed areas. This enabled me to explore within-array responses of the two predators to particular vegetation types (*i.e.*, broccoli or weed).

Although the ground between experimental arrays was kept clear of vegetation by repeated tractor plowing, I tested whether predator responses to treatments were related to treatments in neighboring arrays. To do this, I used a nonparametric test (χ^2) to ask whether treatment arrays whose neighbors on both sides had potentially higher than average numbers of predator defectors had, independent of treatment, higher than average predator densities. For this analysis all arrays for each of the two experimental seasons were characterized by developing an index that reflected their potential for predator emigration to adjacent arrays (*i.e.*, to act as a source for predators to spill over into neighboring arrays). I posited that arrays with high percent crop cover and high fragmentation would be most likely to contribute to "cross-contamination" (these arrays were given a high "neighbor's index" value). For the percent crop cover characteristic, I assigned values of 1 to arrays with 25% crop cover, 2 to arrays with 50% crop cover, and 3 to arrays with 75% crop cover. The rationale behind this ranking was based on the fact that neighbors with more crop cover represent a larger source of predators that may stray next door. My rationale for the formulation of a similar index corresponding to fragmentation scale was that treatment arrays with higher fragmentation contain, by design, crop patches that are smaller than those found in treatment arrays with lower fragmentation for a given percent crop cover, and smaller patches (with larger perimeter to area ratios) generally have higher emigration rates. This reasoning assumes that predators exhibit little or no directed movement within arrays, which is in keeping with the null hypothesis my analysis was designed to test. For this index, I assigned the lowest

Table 1. Output from MANOVA design, performed as a General Linear Model testing for three main effects and one interaction.

	Wilk's λ	*F*	df	*P*
Coccinella septempunctata				
Plot	0.293	2.036	10,24	0.075
Percent crop cover	0.650	0.577	10,24	0.817
Fragmentation	0.020	14.434	10,24	0.000
Percent crop cover × fragmentation	0.303	0.883	20,40	0.607
Pterostichus melanarius				
Plot	0.037	10.063	10,24	0.000
Percent crop cover	0.355	1.631	10,24	0.158
Fragmentation	0.476	1.077	10,24	0.416
Percent crop cover × fragmentation	0.163	1.481	20,40	0.142

Note: Plot represents block replicate within field, percent crop cover indicates percentage of array occupied by broccoli, and fragmentation refers to scale at which patches of broccoli and weeds are fragmented within array. All data were transformed using a Tukey–Freeman square-root transformation to better conform to normality assumptions.

value (1) to arrays with low fragmentation and the highest value (3) to arrays with high fragmentation. For my analyses, the two indices (percent crop cover and fragmentation scale) were added together to generate a combined index. Finally, for each array in both field seasons, the two types of indices of each array adjacent on either side were added to generate an overall neighbor's index. For each array and each sampling date, I tallied whether the neighbor's index was higher or lower than average, and whether the predator density for the array was higher or lower than average in a 2 × 2 contingency table. A χ^2 analysis revealed whether arrays with higher or lower than average neighbor's indices had higher or lower than average predator samples, respectively. This provided a distribution- and treatment-independent method of detecting any biases in overall treatment effects attributable to insects moving across adjacent treatment arrays.

Results

The multivariate analysis of variance revealed that *C. septempunctata* and *P. melanarius* responded differently to vegetation composition and scale of fragmentation. *Coccinella septempunctata* responded to the scale at which broccoli patches were fragmented by weed areas, but not to percent crop cover (Table 1). In contrast, *P. melanarius* did not respond to percent crop cover or fragmentation scale (Table 1). The MANOVA approach is useful in determining the overall effect of the two main treatment factors, but it does not give details about the direction of the differences detected. A graph of the mean number of coccinellids for each level of fragmentation, across all replicates and sample dates, indicates that higher overall densities of coccinellids were found in treatments with the lowest level of fragmentation (Fig. 2). This graph illustrates a directional trend that is stronger in several of the individual univariate responses (see Banks 1999 for more examples).

The MANOVA results indicate that overall coccinellid numbers were not strongly influenced by percent crop cover, although a closer look at the distribution of *C. septempunctata* within treatment arrays reveals a more subtle influence of spatial heterogeneity on predators. The overall mean proportion of the coccinellid within each treatment array found in crop areas, rather than weedy areas, increases monotonically with an increase in percent crop cover (Fig. 3). In all three treatment categories (25, 50, and

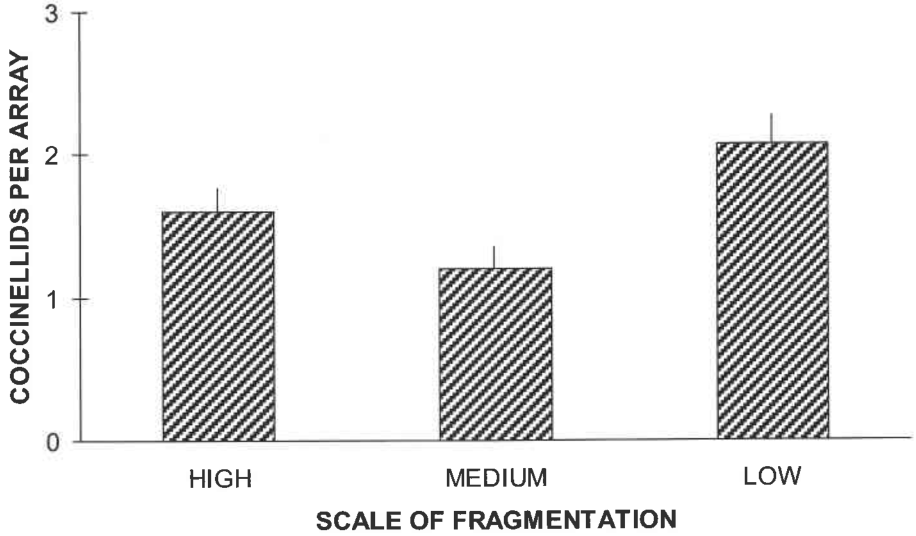

Figure 2. Mean number of *Coccinella septempunctata* per array as a function of fragmentation level averaged over all five sample dates and all fragmentation scales. Bars represent +SE for three means per percent crop cover treatment times three replicates times the number of sampling dates ($n = 45$). Differences were all nonsignificant ($P > 0.05$, Bonferroni pairwise comparison test).

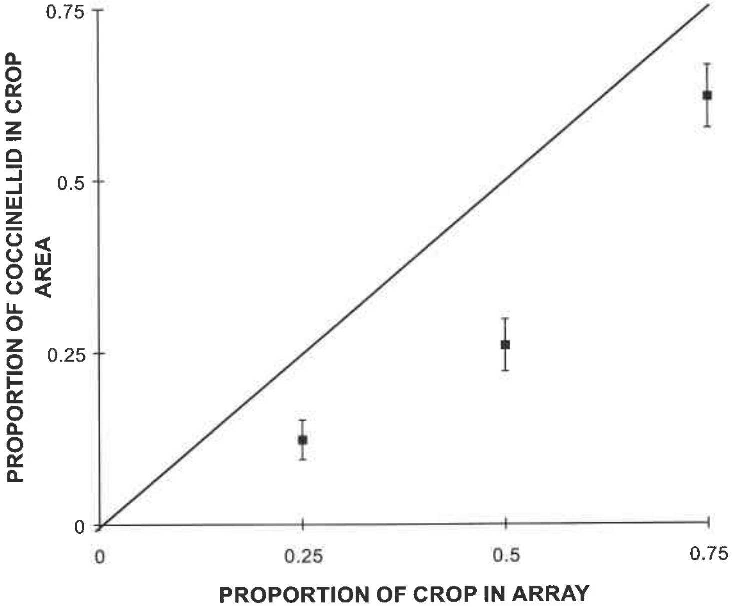

Figure 3. Mean proportion of *Coccinella septempunctata* found in crop areas within treatment arrays, averaged across all five sample dates and levels of fragmentation, as a function of percent crop cover. Arrays in which none of the coccinellid was found were omitted from calculations to avoid artificially underestimating coccinellid proportions in crop areas. Bars indicate ±SE.

75% crop cover) proportions of the coccinellid in arrays are lower than one would expect if the coccinellid were uniformly distributed within arrays. Barring any coccinellid preference for particular vegetation type, one would expect 25% of the sampled

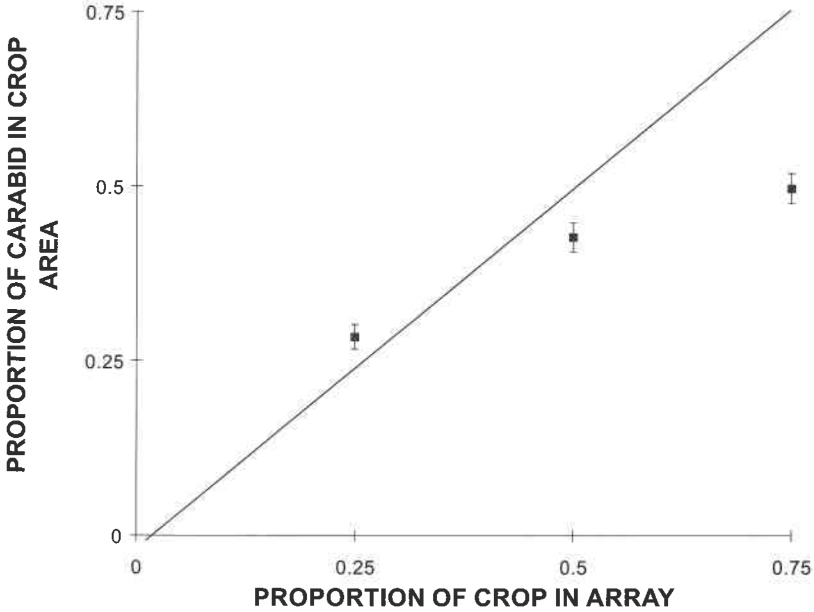

FIGURE 4. Mean proportion of *Pterostichus melanarius* found in crop areas within treatment arrays, averaged across all five sample dates and levels of fragmentation, as a function of percent crop cover. Arrays in which none of the carabid was found were omitted from calculations to avoid artificially underestimating carabid proportions in crop areas. Bars indicate ±SE.

coccinellid population to be found in crop areas in 25% crop cover treatment arrays, 50% of the population to be found in 50% crop cover treatment arrays, and so on. If this were the case, densities of the coccinellid would increase linearly with an increase in percent crop cover, falling on a 45° line (solid line, Fig. 3). Rather, the coccinellid population density consistently fell below the hypothetical 45° line, indicating that the coccinellid was underrepresented in crop areas for all three treatments.

Despite the fact that the MANOVA detected no significant overall treatment effects for the carabid, a more detailed analysis of distributions of *P. melanarius* reveals that, as with the coccinellid, the proportion of the carabid population in crop areas within arrays increases with higher percent crop cover treatments (Fig. 4). Unlike *C. septempunctata*, proportions of the carabid in crop areas exceed proportions predicted for uniform colonization of crop areas in arrays for the smallest percent crop cover treatment (*i.e.*, point lies above the predicted 45° line in Fig. 4). Furthermore, the proportion of the carabid in crop areas diminishes as percent crop cover increases; 29% of the sampled carabid population was in crop areas in 25% crop cover treatments, 43% in crop areas in 50% crop cover treatments, and only 50% in crop areas in the 75% treatments (Fig. 4). Hence the carabid was overrepresented in crop areas only in the weediest treatments.

The χ^2 analysis indicated that the carabid was not influenced by the composition and fragmentation scale of neighboring arrays ($\chi_1^2 = 0.134$, $P > 0.05$); regardless of the specific treatment combination in a particular array, the overall distribution of the carabid did not vary according to the type of arrays adjacent to them. The same analysis, however, indicated that the coccinellid was influenced by the percent crop cover and fragmentation scale of neighboring arrays ($\chi_1^2 = 5.179$, $P < 0.05$).

Discussion

Coccinella septempunctata and *P. melanarius* responded differently to the vegetation composition and scale of fragmentation treatments, thus highlighting the difficulty of generalizing the results of vegetation heterogeneity experiments done for one insect predator to entire assemblages of predators. These results underscore the need to better understand the sensitivity of different predators to vegetation manipulations. One factor that is likely responsible for differences in responses to vegetation diversity such as those revealed in this experiment is that different predators within a single agroecosystem often exhibit very different dispersal behaviors and abilities. These differences may act as a foil to extrapolations of the effects of habitat diversification from a single-predator system to a multipredator system.

The response of *C. septempunctata* to the scale of fragmentation is consistent with prior work done with coccinellids [*i.e.*, increased patchiness has been shown to interfere with the ability of coccinellids to aggregate to prey and to encourage emigration in linear arrays of patchy vegetation (Kareiva 1987)]. The indication that the coccinellid was generally more abundant in my treatments with the lowest fragmentation (Fig. 2) (*i.e.*, treatments with the most continuous patches) may also be due to the fact that in this system *C. septempunctata* is better at foraging for aphids in more continuous areas of crop vegetation. On the other hand, the coccinellid was consistently underrepresented in crop areas of all three percent crop cover treatment arrays (Fig. 3), indicating that although densities were higher in arrays with less fragmentation, individuals were on average preferentially spending time in the weedy areas within those arrays. Given the propensity of coccinellids to feed on pollen (Hagen 1962), it is possible that the coccinellid's response to scale manipulations in this experiment was influenced by large continuous patches of weedy vegetation acting as a pollen source.

The fact that neither the percent crop cover nor the scale manipulations affected the carabid population sampled in this experiment again underscores the fact that insects within a single agroecosystem respond individualistically to vegetation diversification. In this case, it is worth pointing out a few notable features of carabid foraging behavior which present a stark contrast to that of the coccinellid. *Pterostichus melanarius* is much more mobile on the ground than the coccinellid, although its foraging-movement behavior has been shown to be sensitive to hunger levels (Wallin and Ekbom 1994). Furthermore, *P. melanarius* thrives on a more diverse diet, including dipteran and lepidopteran larvae as well as aphids, and will readily forage in both weedy vegetation and crop areas (Chiverton and Sotherton 1991; Wallin *et al.* 1992; Wallin and Ekbom 1994). In addition, tracking and mark–recapture experiments have indicated that *P. melanarius* is equally adept at moving through crop areas and dense weedy vegetation (Wallin and Ekbom 1988), and is not averse to moving across challenging topography such as ridges in planting rows (Gordon and McKinlay 1986; Wallin and Ekbom 1994). Taken together, these behavioral characteristics suggest that *P. melanarius* might not have responded to the broccoli manipulations because individuals were able to move freely through and among all treatment arrays with ease, paying little attention to vegetation structure as they foraged. This result is somewhat unexpected, since *P. melanarius* is sensitive to several factors associated with heterogeneous vegetation structure, including variable vegetation size and density (Cárcamo and Spence 1994) and microclimate (Rivard 1966; Honek 1988).

The results of the χ^2 analysis further indicate that the two predators had different perspectives of the landscape manipulations presented to them in the experimental design. The carabid was unaffected by the characteristics of adjacent treatment arrays, whereas the coccinellid was influenced by neighboring arrays. Although this mechanism alone cannot explain the significant response of the coccinellid to the fragmentation-scale manipulations detected by the MANOVA (because treatment arrays were randomly arranged within each block, combinations of neighbors were different for each array in each replicate), it reinforces the notion that the coccinellid may be perceiving the landscape as more coarsely grained than the carabid. That is, the coccinellid, with it's largely foliar foraging behavior, may be influenced not only by local vegetation composition and fragmentation scale, but also by the vegetation composition and fragmentation scale in nearby plots, responding to a larger mosaic of several different arrays at once. Once again, this response highlights the difficulty in assessing the effects of vegetation diversity on more than one predator species at a time.

One important component of predator response to vegetation diversity which was not directly explored in this experiment is aggregation to prey. Both coccinellids and carabids aggregate to prey items (Bryan and Wratten 1984; Carter and Dixon 1984); in the broccoli agroecosystem described here both predators feed on several phytophagous insects, including several aphid species. In a related experiment, I assessed the response of the predominant aphid species, the cabbage aphid *B. brassicae*, to the same vegetation-diversity manipulations conducted in the present experiment (Banks 1998). Results from that experiment indicate that percent crop cover but not fragmentation scale influenced the distribution of *B. brassicae*. Although time and resources prevented sampling of predators and aphids at the same time in the experimental arrays, precluding a meaningful comprehensive cross-correlation analysis of predator and prey distributions, these contrasting results suggest that the predator responses to vegetation-diversity manipulations cannot be explained simply by prey distributions. Thus, the coccinellid's response to fragmentation scale but not percent crop cover is likely attributable to a range of biotic and abiotic factors such as dispersal behavior and microclimate and is not simply a response to the distribution of prey.

Other aspects of this experiment that might have biased the results and complicate interpretation are associated with the experimental design and sampling techniques. The narrow width of the plots, although consistent for all treatments, could have introduced an "edge effect" that might have affected the natural enemy populations in a variety of ways, including changes in dispersal, mortality, and interspecies and intraspecies interactions (Fagan *et al.* 1999). Furthermore, pitfall traps have long been used to measure carabid activity (Greenslade 1964), but there are problems inherent in correlating pitfall catches with carabid densities, even for the purpose of comparing relative abundance in different habitats (Niemelä *et al.* 1988). These complications must be considered in making quantitative assessments of the response of each of the two predators to the experimental manipulations, although they do not detract from the qualitative difference in the responses of the coccinellid and the carabid. Of course, these complicating factors would warrant close examination in any follow-up attempts to generate applied protocols for recommending actual deployment of weed–crop mixtures to growers.

Although this experiment was designed to analyze the effects of vegetation diversity on the two predators independently of each other, it is worth noting recent work that documents interactions between *C. septempunctata* and carabid beetle predators in controlling insect herbivore pests (Losey and Denno 1998*b*). Although in many instances the effects of multiple predators on pest populations is additive (Chang 1996), in some cases foliar-foraging predators may disturb pests to the extent that pest-evasive behavior increases their susceptibility to ground-dwelling predators. This type of synergism, coupled with differential predator responses to vegetation manipulation, further complicates efforts to make general characterizations of the effects of habitat diversity on natural enemies in agroecosystems.

Finally, from an applied perspective, it is important to bear in mind that simple increases in predator densities in diversified habitats do not guarantee an automatic reduction in pest populations (Colunga-Garcia *et al.* 1997). The fact that relatively small proportions of the coccinellid and the carabid (at higher percent crop covers) were found in crop areas within arrays (Fig. 3) serves as a reminder that these results are merely preliminary. Further detailed observational–behavioral data are needed in conjunction with the distribution data provided by this experiment to gauge how effective a strategy it might be to increase weediness in and around crop areas to enhance control of pest insects by these predators.

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