Effects of plot vegetation diversity and spatial scale on *Coccinella septempunctata* movement in the absence of prey

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Abstract

The influence that vegetation diversity and the spatial scale of that diversity exert on insect behavior has increasingly been explored in the ecological literature, but relatively few experiments have explicitly incorporated both factors in experimental treatments. We conducted a field study designed to explore the effect of both of these factors on insect movement behavior in a broccoli agroecosystem. We caught and released seven-spotted ladybird beetles (*Coccinella septempunctata* L.) in plots containing different degrees of vegetation diversity at two different spatial scales in which prey had been removed. Beetle movement was recorded at timed intervals, and move lengths and turning angles were used to generate discrete path maps for each beetle. Observed mean beetle net squared displacements were compared with predicted net squared displacements, and 95% confidence intervals were generated using a bootstrap method described by Turchin (1998) [Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinauer Associates Inc., Sunderland, MA.]. Predicted net squared displacements underestimated beetle movement in smaller plots with both low and higher vegetation diversity for the first five move lengths, whereas no significant difference between observed and predicted net squared displacement for beetles in larger plots of either level of vegetation diversity were detected. These findings highlight the need for a better understanding of how natural enemies are influenced by vegetation diversity and the spatial scale of that vegetation in agroecosystems. The implications of these results for biological control are discussed.

Introduction

Insect ecologists have long been concerned with the influence that vegetation heterogeneity exerts on population abundance and distribution (Root, 1973; Cromartie, 1975; Bach, 1980a,b; Horn, 1981; Kareiva, 1985; Vandermeer, 1989; Bohlen & Barret, 1990; Johnson et al., 1992; Carcamo, 1995; Banks, 1998, 1999, 2000; Banks & Ekbom, 1999; Doak, 2000). While insights gleaned from these studies have contributed greatly to our understanding of how ecological processes mesh with both biotic and abiotic factors via habitat vegetation structure and composition, they have been largely focused on the relationship between herbivorous insects and vegetation spatial patterning and diversity. Of the much smaller number of studies exploring the link between natural enemies and their habitats, most have been measured indirectly in terms of predator–prey–habitat interactions (Root, 1973; Cromartie, 1975). Notable exceptions are recent studies of parasitoid-host dynamics (e.g., Roland & Taylor, 1997) that have demonstrated that host–parasitoid interactions are sensitive to host distribution as well as to the structure and composition of host habitat. However, less is known about the response of less specialized predators such as polyphagous beetles to vegetation structure (but see Kareiva & Perry, 1989; Crist et al., 1992). Although the aggregation of beetles to their prey has been the subject of much recent important theoretical and experimental work (Bryan & Wratten, 1984; Kareiva & Odell, 1987; Grünbaum, 1998; Raymond et al., 2000), these studies lend little insight into how the physical characteristics of vegetation habitat, independent of prey densities, may directly influence predator behavior and subsequent abundance and distribution.

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The importance of spatial scale in ecological phenomena has received much attention in the past few decades (Murphy, 1989; Wiens, 1989; Rose & Leggett, 1990; Dwyer, 1992; Levin, 1992; Durrett & Levin, 1994; Holmes et al., 1994; May, 1994; Molumby, 1995; Underwood & Chapman, 1996; Tilman & Kareiva, 1997). Despite this trend, there have been relatively few field experiments that explicitly incorporated scale as a manipulated treatment factor (Rothman & Darling, 1991; Marino & Landis, 1996; Schooler et al., 1996; Roland & Taylor, 1997; Banks, 1998, 1999; Norowi et al., 2000). One means of exploring the effects of spatial scale on ecological interactions is by quantifying the movement patterns of organisms in habitats of different scales; insects are especially amenable to this sort of analysis (Cain et al., 1985; Wiens & Milne, 1989; Turchin et al., 1991; Wiens et al., 1993a,b; Turchin, 1998).

We describe here field experiments that expressly examined how habitat vegetation diversity and the spatial scale of that diversity exert direct effects on predator behavior. In particular, our experiments aimed to quantify the response of polyphagous beetles directly to habitat manipulations in the absence of their prey. In order to disentangle predator aggregation behavior and their response to vegetation diversity, we removed all prey in the experimental plots by spraying plants with a selective pesticide prior to conducting our experiments. Using a diffusion model (correlated random walk) commonly used to describe insect movement, we then compared the behavior of the common seven-spotted ladybird beetle (*Coccinella septempunctata* L.) (Coleoptera: Coccinellidae) in plots with two levels of vegetation diversity at two different spatial scales. We discuss the ramifications of our study in agricultural settings, especially in relation to biological control.

Materials and methods

Coccinella septempunctata

Coccinella septempunctata, the seven-spotted ladybird beetle, is a common aphidophagous predator that was introduced to the USA in the 1950s, and has since become ubiquitous, although the details of its establishment are not precisely known (Angalet et al., 1979; Schaeffer et al., 1987; Elliott et al., 1996; Obrycki & Kring, 1998). *Coccinella septempunctata* will consume aphids and other insects, but is also attracted to pollen and nectar (Hagen, 1962). Individuals typically fly among patches of vegetation searching for likely prey habitat, then switch to a walking behavior once they have alighted and begin foraging (Hodek, 1973). Once in prey habitat, beetles cue on aphid presence, often resulting in increased oviposition and large aggregations of ladybirds near prey (Evans & Dixon, 1986; Obrycki & Kring, 1998).

Field experiments

We established plots of broccoli (*Brassica oleracea*, var. Emporer F1, Zenner Bros., Oregon) at two different spatial scales surrounded by either bare ground or weedy vegetation at Washington State University's Puyallup Research and Extension Center Experimental Farm Five, 70 km south of Seattle in Puyallup, Washington, USA. Broccoli was used in this experiment because it can be grown in homogeneous stands of relatively uniform plants. Broccoli were established in square plots measuring either (i) 2.5 m × 2.5 m (smaller scale), or (ii) 5 m × 5 m (larger scale). Plots at both spatial scales were planted with low or high vegetation diversity, surrounded in each case by 1 m or 2 m wide (respectively) margins of either (a) bare ground, or (b) weedy vegetation. At both spatial scales, broccoli were spaced 0.5 m apart; smaller-scale plots contained 16 (4 × 4) broccoli plants, while larger-scale plots contained 64 (8 × 8) plants. The most prevalent species in weedy margins were *Amaranthus powellii* (S. Watson), *Chenopodium album* (L.), *Echinochloa coluna* (L.), and *Echinochloa crus-galli* (L.). All plots were separated from other plots by a minimum of 5.5 m in order to ensure that insect movements within plots were independent of neighboring plots in the field. Weedy vegetation in-between plots and within broccoli areas of each plot was regularly removed by tractor and hand cultivation, respectively, throughout the duration of the experiments.

Broccoli were grown from seed in moulded polypropylene planting flats and kept in the greenhouse until large enough to transplant into the field. Smaller-scale plots were established in the field on 19 June 2000; broccoli were transplanted into larger-scale plots on 24 July. Because broccoli attracts a suite of herbivorous aphids in western Washington, including *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* (L.), all broccoli plants in experimental plots were sprayed with the selective pesticide Pirimor on 27 July. We removed the aphid prey so that behavioral experiments could be conducted without prey as a confounding factor in beetle response to vegetation manipulations. In order to minimize possible effects of residuals on experimental ladybirds, we waited 5 days before doing any movement behavioral experiments. Subsequently, throughout the duration of the experiment, plants were frequently checked to minimize the possibility that there were aphids on any of the broccoli plants.

Data collection

For the behavioral observation experiments, we collected live *C. septempunctata* individuals from vegetation adjacent to the experimental plots and placed them singly in cardboard containers. Beetles were kept in the containers in a cool, shaded area in the field before being observed in broccoli plots. Special care was taken not to keep beetles in the containers for more than 1 h before using them in behavioral experiments to minimize possible changes in their behavior due to being held captive too long; in most cases, they were kept no longer than 15–20 min in containers. Each individual was released on the ground in the center of a randomly chosen weedy margin or bare ground margin plot and its subsequent movement behavior recorded. As soon as a beetle began moving, we began marking its positions at 5 s intervals, placing thin pieces of wire with numbered flags on the ends into the ground at each position, keeping well out of the way to be sure the beetles were not disturbed by our marking activity. After 10 5-s moves were completed, we measured net squared displacements and the move lengths and turning angles from each previous direction for all moves. We recorded a total of 24 beetle paths in smaller plots (14 bare ground, 10 weedy), and 30 beetle paths in larger plots (15 bare ground, 15 weedy), for a total of 54 beetles used in the study.

Movement model

We used a diffusion model to quantify beetle behavior in the different treatment settings. In particular, we used a random walk model that stipulates that the beetles move randomly with some tendency to move in the same direction from one move to the next. The model, a modified simple diffusion model originally developed by Goldstein (1951), may be described as:

$$\frac{\partial^2 p}{\partial^2 t^2} + \frac{2}{T}\frac{\partial p}{\partial t} = v^2 \frac{\partial^2 p}{\partial x^2}$$

where p is the particle (or beetle) density, v is the wave speed (a measure of how fast the population is diffusing) and T is a characteristic move correlation time (particular to the correlation among moves for beetles) (Okubo & Grünbaum, 2001). This model, known as the telegraph equation, or more generally as a correlated random walk (CRW) model, has been employed in several other insect movement studies, including those modeling beetles (Kareiva & Shigesada, 1983; Wallin & Ekbom, 1988; Turchin, 1991, 1998; Crist et al., 1992). Because it allows for some correlation in the direction of turning of successive moves, it is a more realistic description of the behavior of many foraging insects than a simple random walk. Furthermore, it is also mathematically more realistic for terrestrial insects, predicting a finite dispersion velocity rather than the infinite velocity characteristic of simple random walks (Okubo & Grünbaum, 2001).

Analysis

In order to test the fit of observed beetle movement to the CRW model in different treatment settings, we compared observed mean net squared displacements for each beetle, $\bar{R}_n$, to predicted mean net squared displacements. We generated the predicted $\bar{R}_n$, and corresponding 95% confidence intervals using 10 000 runs of a bootstrap simulation described by Turchin (1998), in which we repeatedly sampled move lengths and turning angles with replacement from the pool of observed data collected for each treatment. We made these comparisons for low and high vegetation diversity (bare ground and weedy margins, respectively) plots, for both smaller and larger scale experimental plots. Autocorrelation in turning directions was tested by developing contingency tables based on correlated subsequent turn directions: left-left, left-right, right-right, and right-left for bare ground and weedy plots at each spatial scale. Autocorrelation in move lengths was analyzed by calculating Pearson product-moment correlation coefficients using subsequent lengths for bare ground and weedy plots separately at each scale. Differences in frequency distributions for turning angles in bare ground and weedy plots at both scales were analyzed using the Mann–Whitney nonparametric test (Sokal & Rohlf, 1995).

Results

Beetles exhibited a strong response to the experimental plot spatial scale manipulations, but not to the vegetation diversity treatments. In particular, in the smaller-scale plots, observed mean net squared displacement in the bare ground plots did not fall within the 95% confidence limits until after five moves (Figure 1), whereas in larger-scale plots, observed and predicted mean net squared displacements both fell completely within the confidence intervals (Figure 2). The responses of the beetles at both spatial scales were qualitatively similar for both bare ground and weedy plots, suggesting that margin vegetation had little influence on beetle dispersal.

We found no autocorrelation in direction of movement for either bare ground or weedy margin plots at either scale (small bare ground: $\chi^2 = 0.216$, $P > 0.1$, $n = 51$; small weedy: $\chi^2 = 0.365$, $P > 0.1$, $n = 39$; large bare ground: $\chi^2 = 1.167$, $P > 0.1$, $n = 56$; large weedy: $\chi^2 = 0.117$, $P > 0.1$, $n = 48$). Furthermore, we found no autocorrelation in move lengths for larger plots for bare ground plots (Pearson correlation coefficient = 0.001, $P > 0.1$, $n = 120$) but did find some autocorrelation in move lengths in weedy plots (Pearson correlation coefficient = 0.270, $P < 0.005$, $n = 120$). For smaller plots, there was evidence of move length autocorrelation for both bare ground (Pearson correlation coefficient = 0.736, $P < 0.001$, $n = 112$) and

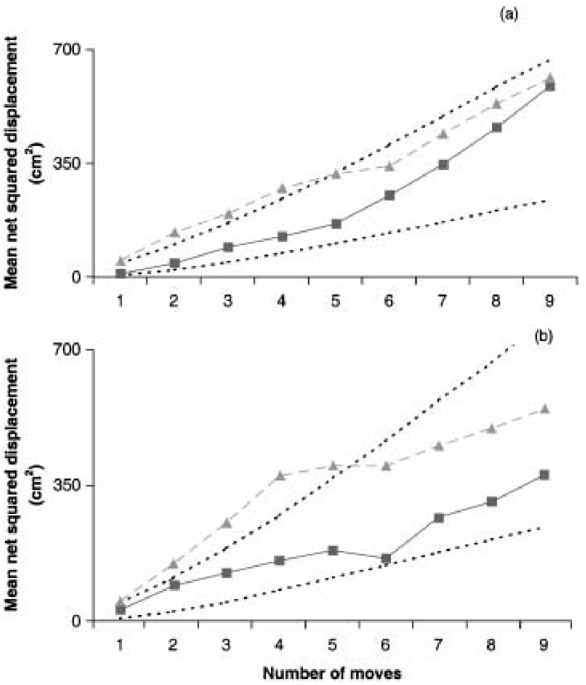

Figure 1 Comparison of observed (dashed line with triangles) and predicted beetle mean net squared displacement (solid line with squares) at smaller spatial scale in: (a) bare ground margin plots, and (b) weedy margin plots. Predicted mean squared displacement and 95% confidence intervals (dotted lines) were obtained by simulation (see text).

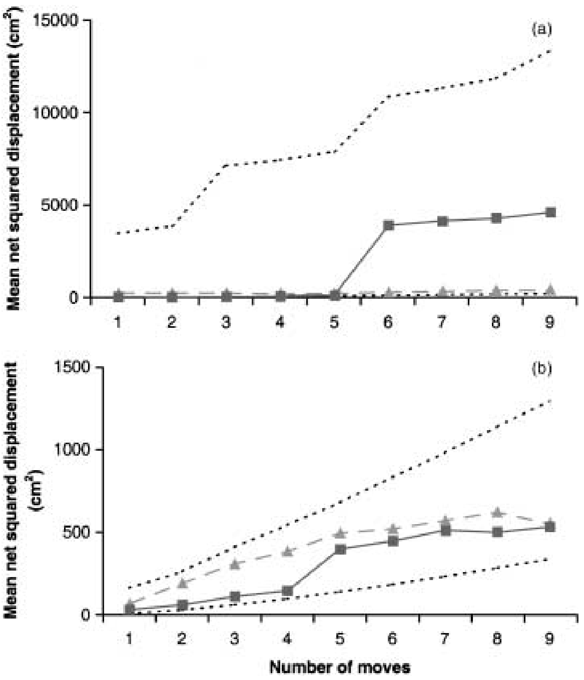

Figure 2 Comparison of observed (dashed line with triangles) and predicted beetle mean net squared displacement (solid line with squares) at larger spatial scale in: (a) bare ground margin plots, and (b) weedy margin plots. Predicted mean squared displacement and 95% confidence intervals (dotted lines) were obtained by simulation (see text).

weedy plots (Pearson correlation coefficient = 0.653, P < 0.001, n = 80).

The frequency distribution of turning angles did not differ significantly between margin types in smaller plots (U = 2130.5, P = 0.74, n = 134) (Figure 3) or larger plots (U = 2447, P = 0.494, n = 137) (Figure 4). Likewise, there was no difference in move length frequency distributions between margin treatments for smaller plots (U = 5403.5, P = 0.551, n = 216) or larger plots (U = 8009.5, P = 0.082, n = 270).

Discussion

Our results indicate that coccinellid movement depends more strongly on the spatial scale of the experimental plots than on the diversity of the vegetation present. These findings serve as a cautionary note for those trying to interpret the abundance and distribution patterns of predator–prey complexes in ecological field experiments conducted at different spatial scales.

Past greenhouse/field studies have shown that plant architecture may have a marked effect on how ladybird beetles interact with prey (Kareiva & Perry, 1989; Grevstad

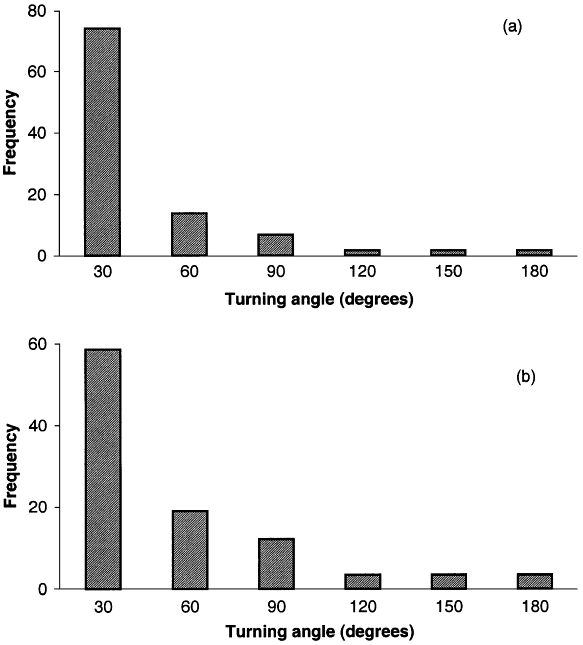

Figure 3 Frequency distribution of turning angles at smaller spatial scale in: (a) bare ground margin plots, and (b) weedy margin plots.

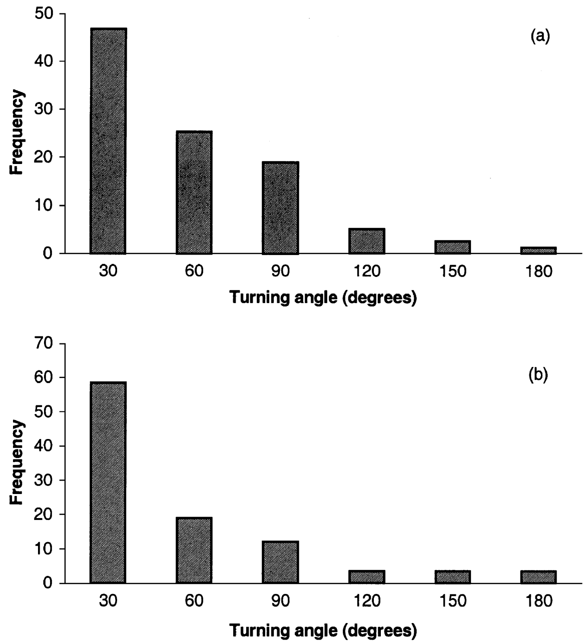

Figure 4 Frequency distribution of turning angles at larger spatial scale in: (a) bare ground margin plots, and (b) weedy margin plots.

& Klepetka, 1992). However, the current study represents one of the first field studies aimed at directly measuring beetle movement strictly in response to vegetation diversity and spatial scale in the absence of prey. Previous studies have demonstrated that ladybird beetles respond to both chemical and visual cues when searching for prey (Obata, 1986; Harmon et al., 1998), with some species relying on long-distance visual acuity to identify and move towards plants (Lambin et al., 1996). The difference in movement behavior between the two scales of our experimental plots suggests that *C. septempunctata* may be limited in their ability to orient using visual and chemical cues beyond a certain distance. Our data suggest that this distance may lie somewhere between 1 and 3 m, corresponding to the mean distance from the center of our plots to the edge of the margin somewhere between the small and larger scales. Independent of this speculation regarding underlying mechanisms, our results demonstrate that simple characterizations of ladybird beetle movement within agroecosystem habitat patches are not forthcoming.

There are several possible reasons why the correlated random walk model underestimated the mean net squared displacement of beetles in the first five moves of the observations in the smaller scale plots. The first, of course, is that beetles in smaller scale plots initially move straighter and farther from their point of origin than we would expect in a correlated random walk, suggesting that they are able to orient towards distances beyond the boundaries of the experimental plots. A second possibility, against which Turchin (1998) cautions, is that move lengths may have been oversampled, leading to the inadvertent lumping together of some autocorrelated moves in the early part of the paths. Indeed, the detected autocorrelation in move length suggests that this artefact may have contributed to this pattern. However, in both weedy and bare ground margin plots in the small scale experiments, this difference disappears in the second half of the mean net squared displacements, indicating that the CRW is, on average, a good fit for the latter half of the paths. Furthermore, in larger plots, the observed paths do fit the CRW model, despite the fact that the same beetle release protocol and broccoli spacing within plots were the same as in the smaller scale observations. This discrepancy suggests that beetles are responding to inherent differences in landscape features at the two scales – which may or may not be in part a function of their range of visual or chemical sensory capabilities. Numerous studies have illustrated that the spatial details of vegetation diversity are important to herbivorous prey colonization and abundance (Bommarco & Banks, 2003, Risch et al., 1983; Banks, 1998; Ferguson et al., 2003). Further similar field studies investigating the interplay of visual and chemical cues and landscape features at different scales need to be conducted to better understand how these factors combine to determine ladybird response to host plant vegetation both with and without prey.

The literature is replete with evidence that coccinellid movement behavior is influenced by the consumption of prey, resulting in 'area-restricted' or 'area-concentrated' searching behavior (Banks, 1957; Carter & Dixon, 1982; Nakamuta, 1982, 1985). Such intensive foraging behavior stimulated by the ingestion of prey can lead to macroscopic patterns of 'preytaxis', in which beetles aggregate to prey and even control outbreaks (Kareiva & Odell, 1987). Furthermore, in the absence of sufficient prey, as is the case in the current experiment, beetles have been shown to increase their movement rates (Wallin & Ekbom, 1994; Firle et al., 1998). In such cases, which correspond to natural enemies colonizing fields before prey reach appreciable numbers, coccinellids failing to encounter any prey items may move out of broccoli patches more quickly (i.e., move less randomly) than we might expect. This may explain why the CRW underestimated beetle movement in our smaller plots (Figure 1); however, it does not explain why this underestimate did not hold true for the larger-scale plots, nor why there is a difference in behavior between the two spatial scales. These results may have some bearing on a common scenario in agroecosystems in which primary prey emergence occurs much later than the arrival of natural enemies, especially in the absence of early season alternative prey (Settle et al., 1996). The properties of this type of asynchrony, familiar to biological control practitioners attempting augmentative releases, have been the basis of much theoretical work in time lags and the stability of predator–prey interactions (Hutchinson, 1948; May, 1974; Cushing, 1977; Nisbet & Gurney, 1982). In light of this body of theory, we might expect the stability of beetle-aphid cycles to be a function of the scale of the habitat in which they interact. However, as Cain (1991) pointed out, there are limitations to the extrapolation of diffusion-based analyses to predictions at larger spatial and temporal scales.

The difference we saw in our experiments in beetle responses for each spatial scale suggested that edge-mediated behavior may be important in understanding coccinellid behavior and foraging capabilities within and around crop fields. The influence that habitat edges may have upon local within- or between-habitat patches has recently become the subject of much interest in both theoretical and field-experimental circles (Fagan et al., 1999; Cantrell et al., 2001; Schultz & Crone, 2001; Bommarco & Fagan, 2002). In particular, in addition to moving differently within habitat patches (i.e., experimental plots), beetles may change their movement behavior as they approach the boundary of the habitat (Bommarco & Fagan, 2002).

Some of our previous work has shown that *C. septempunctata* preferentially colonizes weedy vegetation (which often offers an array of nectar resources) in weed-crop intercrops (Banks, 1999). Similarly, van der Werf et al. (2000) found that *C. septempunctata* readily aggregate to sugar-sprayed weedy vegetation, although prey density and plant volatiles acted as additional colonization cues in that study. While the present experiment was not designed to gauge how beetles perceive their proximity to the edge of the habitat plots or the quality of neighboring patches, our results highlight the need for a better understanding of how landscape features affect beetle movement. In particular, these results suggest that the spatial details of augmentative releases of biological control agents (apart from the overall spatial scale of plots in which they are released) – especially the proximity of their release to habitat boundaries or edges – may be critical to successful predator retention in the habitat and the success of the control effort.

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