Refuge habitats modify impact of insecticide disturbance on carabid beetle communities

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Summary

1. Carabid beetles are polyphagous predators that can act as biological control agents of insect pests and weeds. While current agricultural practices often create a harsh environment, habitat management such as the establishment of within-field refuges has been proposed to enhance carabid beetle abundance and impact. We examined the joint effects of refuge habitats and insecticide application on carabid activity density (parameter of population density and relative activity) and species composition in a cornfield.

2. Our 2-year study comprised four treatments: (i) –refuge/–insecticide; (ii) +refuge/–insecticide; (iii) –refuge/+insecticide; (iv) +refuge/+insecticide. Refuge strips consisted of grasses, legumes and perennial flowering plants. '–Refuge' strips were planted with corn and not treated with insecticide.

3. Before planting and insecticide application, carabid activity density in the crop areas was similar across all treatments. Insecticide application immediately reduced carabid activity density and altered community composition in the crop area.

4. Refuge strips had significantly higher activity density of beetles than –refuge strips before planting and during the summer.

5. During summer, as new carabids emerged and insecticide toxicity declined, the presence of refuge strips influenced carabids in the adjacent crop area. Carabid activity density within crop areas previously treated with insecticide was significantly higher when adjacent to refuge strips. Also, carabid communities within insecticide-treated crop areas were affected by the presence or absence of a refuge strip.

6. The presence of refuge strips did not consistently augment carabid numbers in crop areas where insecticide was not applied. One explanation may be that insecticides decreased the quality of crop habitat to carabids by depletion of prey and direct mortality. However, subsequent rebounds in prey density and the absence of competing predators may make these areas relatively more attractive than unperturbed crop habitats to carabid colonization from refuges.

7. This study demonstrates that refuges may buffer the negative consequences of insecticide application on carabids in adjacent fields. Diversifying agro-ecosystems with refuge habitats may be a viable strategy for maintaining carabid populations in disturbed agricultural landscapes to keep pests below outbreak levels.

Key-words: agro-ecosystem, biological control, diversification, habitat management.

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Introduction

Agricultural landscapes are increasingly being simplified and undergo frequent and intense disturbances such as harvest and the input of chemicals; these factors have been postulated as contributing to failed establishment of natural enemies and biological control programmes (Landis & Menalled 1998). Several studies have shown that the degree of complexity is a critical factor in moderating natural enemy abundance in agricultural landscapes (Halley, Thomas & Jepson 1996; Marino & Landis 1996; Menalled *et al.* 1999; Thies & Tscharntke 1999), diversity (Gut *et al.* 1982), and fecundity (Bommarco 1998). Agricultural practices including insecticide application act as disturbances, reducing natural enemy populations and species richness (Los & Allen 1983; Booij & Noorlander 1988;

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Croft 1990). Repeated insecticide inputs result in the dominance of a few tolerant species, thereby changing natural enemy communities in the long term (Menhinick 1962; Burn 1989; Basedow 1990). Disruption of natural enemy complexes ultimately leads to reduced pest control (Edwards, Sunderland & George 1979; Brust, Stinner & McCartney 1985, 1986). Understanding the impacts of common agricultural practices and habitat complexity on natural enemies is critical in developing ecologically based pest management (Landis, Wratten & Gurr 2000).

Carabid beetles are common predators in agro-ecosystems and consume a wide variety of arthropod pests, weed seeds and slugs (Sunderland 1975; Lund & Turpin 1977a; Asteraki 1993). The abundance of carabids in crop fields has been positively correlated with prey removal rates (Menalled, Lee & Landis 1999) and with a reduction of crop damage by various agricultural pests (Wright, Hughes & Worrall 1960; Wyman, Libby & Chapman 1976; Lovei & Sunderland 1996). Although agricultural practices may limit carabid beetle populations (Clark, Gage & Spence 1997), increasing habitat complexity on the farm may ameliorate these effects (Bommarco 1998). Agro-ecosystem complexity can be increased by maintaining undisturbed vegetative refuge habitats such as nearby grasslands, hedgerows, field margins and grassy strips within a field. These refuge habitats provide ground beetles with overwintering sites (Desender 1982; Sotherton 1984), alternative prey (Hawthorne & Hassall 1995) and may act as a spring–summertime shelter (Lys, Zimmerman & Nentwig 1994; Thomas *et al.* 2001). Consequently, the abundance, species richness, survivorship and fecundity of adult carabids have been reported to be higher in refuge habitats than in crop fields (Dennis, Thomas & Sotherton 1994; Lys & Nentwig 1994; Zangger, Lys & Nentwig 1994; Thomas & Marshall 1999). Moreover, the presence of a refuge may enhance carabid abundance and species richness in the adjacent field (Coombes & Sotherton 1986; Frank 1997).

Despite the importance of refuge habitats and disturbances in regulating carabid abundance and communities in agro-ecosystems, the interaction between these two factors is not well understood. In this study, we attempted to determine if refuge habitats can act as a source of carabids to colonize adjacent fields, thereby mitigating the consequences of insecticide disturbance. We hypothesized that insecticide application will deplete carabid activity density, lower species richness and alter community composition, but that the presence of a refuge will allow carabid assemblages to recover more rapidly in disturbed crop areas.

Materials and methods

SITE DESCRIPTION AND SAMPLING

This 2-year study was conducted at the Entomology Research Farm, Michigan State University, East
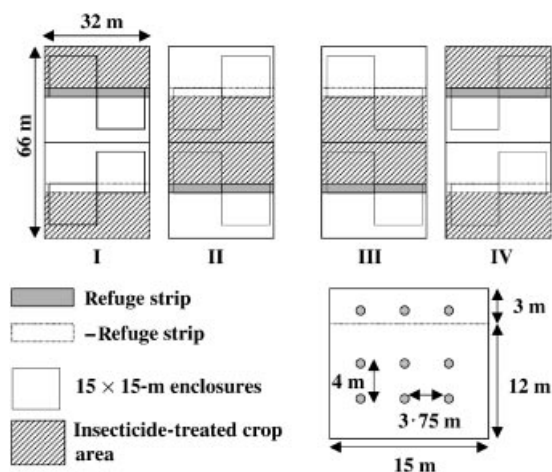
Fig. 1. Map of the experimental site in 1998 and 1999, Michigan State University, East Lansing, Michigan, USA. The total area was 1·4 ha. A diagram of the pitfall trap arrangement is also shown.

Lansing, Michigan, USA. The 1·4-ha site was arranged in a split-plot design with four 32×66-m blocks (Fig. 1). Each block contained two main plots, one with a 3-m wide refuge strip in the centre and the other with a control (–refuge) strip planted with corn *Zea mays* L. (Pioneer 3573). The refuge strips were established in 1995 using orchard grass *Dactylus glomerata* L., white clover *Trifolium repens* L. and a mix of perennial flowering plants to provide supplementary food for predators and parasitoids (Carmona & Landis 1999). On 22 May 1998 and 13 May 1999, corn was planted in rows spaced 76 cm apart. Main plots were divided into two subplots, one of which was treated with insecticide. Refuge and –refuge strips did not receive insecticide. The soil insecticide terbufos (S-[[(1,1-dimethylethyl) thio] methyl]; Counter™ 20 CR, American Cynamid Co., New Jersey, USA) was applied once at the recommended rate of 170·1 g 304·8 m^{-1} in an 18-cm T-band during planting (1·44 kg active ingredients ha^{-1}). In the USA midwest, terbufos is commonly used in non-rotated corn to control corn rootworm larvae *Diabrotica* spp. and is toxic to carabid beetles (Gholson *et al.* 1978). Four treatments were established and referred to as: (i) –refuge/–insecticide; (ii) +refuge/–insecticide; (iii) –refuge/+insecticide; (iv) +refuge/+insecticide. To prevent cross-plot movement of carabids and to isolate treatments, barriers comprising plastic sheeting (15×15 m in perimeter, 15 cm below-ground and 20 cm above-ground) were set up within 1 week of planting and insecticide application (Fig. 1). Barriers established in 1998 remained in place over the winter and spring of 1999 and were removed only prior to planting in 1999. Ground-level barriers have been used effectively to control carabid dispersal (Holliday & Hagley 1978; Edwards, Sunderland & George 1979; Chiverton 1987; Holland, Thomas & Hewitt 1996; Holland 1998; Menalled, Lee & Landis 1999).

Adult carabids were sampled with pitfall traps (11-cm diameter, 934-cm^3 plastic cups with the rim 1 cm

below the surface). No killing agent was used in the traps, to maintain populations within the enclosed plots. Each plot had nine pitfall traps spaced at least 3·75 m apart, with three traps in the strip and six traps in the crop area (Fig. 1). Every 14 days, between April and October in 1998 and March and September in 1999, traps were opened for four consecutive nights and checked each morning. Repeated sampling minimized potential fluctuations of carabid activity due to night-to-night weather changes (Honek 1988, 1997; Thomas, Parkinson & Marshall 1999). Carabid beetles were counted, identified to species (Lindroth 1969) and released immediately back in the same plot. Samples were pooled into three time periods: (i) before planting (21 April–6 May 1998, 31 March–27 April 1999); (ii) after planting (2 June–17 June 1998, 25 May–8 June 1999); (iii) summer–autumn (2 July–6 October 1998, 25

June–14 September 1999) (Fig. 2a,b). By comparing carabid assemblages before planting we were able to assess the field before experimental manipulation. Carabids captured for 1 month after planting and insecticide application allowed us to evaluate the immediate effects of terbufos toxicity because terbufos remains active in the soil for several weeks (Harris 1977; Lesiewicz, Van Duyn & Bradley 1984). Carabids captured during the summer–autumn period served to assess season-long effects of terbufos and refuge habitats on carabids.

ACTIVITY DENSITY

The number of carabids captured in pitfall traps is a measure of the activity density of carabids (Greenslade 1964; Thiele 1977). Activity density of carabids was evaluated in the refuge or –refuge strips by summing all
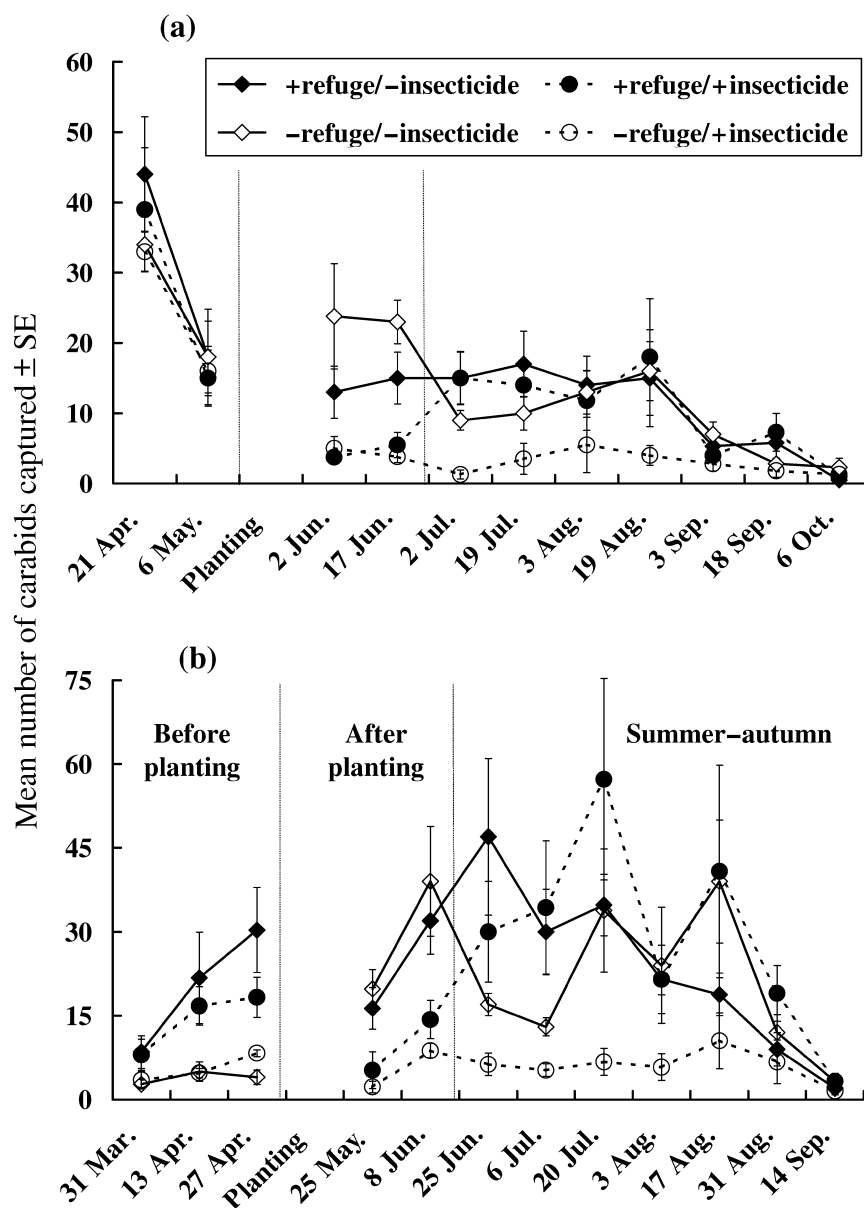

Fig. 2. Mean activity density of carabids ± SE in the entire plot (combining strip and crop area) of the four treatments. (a) 1998; (b) 1999.

beetles captured from the three traps positioned in the strips over the particular time period. Likewise, activity density in the crop area was obtained by summing all beetles captured from the six traps over the time period. Direct comparisons between beetles captured in strips vs. crop areas were not made because sampling efforts were different in the respective areas. To evaluate carabid activity in refuge vs. crop vegetation, beetles captured in refuge strips were compared to –refuge strips. To evaluate insecticide toxicity, captures in crop areas with and without insecticide were compared.

The total numbers of beetles captured in an area (strip or crop area) during each time period were square-root transformed before analysis to normalize variances. Refuge, insecticide and refuge × insecticide effects on activity density were tested using a split-plot analysis of variance, with refuge as the whole-plot factor and insecticide as the split-factor. Also, simultaneous multiple comparisons between the four treatments were conducted using least-significant difference tests (LSD) on their least-square means (PROC MIXED; SAS Institute 1996). Differences were considered significant when $P < 0.05$ and marginal when $P < 0.1$.

SPECIES RICHNESS AND COMMUNITY COMPOSITION

Species richness within the crop area of the four treatments was also compared at each time period. As the number of beetles varied among treatments possibly affecting the number of species collected, species richness was adjusted for sample size using the Menhinick index [number of species/(sample size)$^{1/2}$] and analysed in a split-plot analysis of variance (JMP®; SAS Institute 1995). Variations of carabid community composition within crop areas due to refuge presence and insecticide application were evaluated using detrended correspondence analysis (DCA) (Hill & Gauch 1980; McCune & Mefford 1995). DCA uses a matrix on the abundance of each species at each site and ordinates the sites on multiple axes; the first DCA axis represents the most significant source of variation. Thus, sites with similar species composition will be closer together on a two-dimensional graph. Each unit represents one standard deviation, such that 100 standard units generally signifies a 50% change in species composition (Gauch 1985). For every time period, DCA axis 1 and 2 scores were tested for correlation with the presence of an adjacent refuge, use of insecticide and combination of refuge × insecticide to determine their importance in shaping the overall community (Quinn, Halbert & Williams 1991). DCA axis scores were correlated with refuge × insecticide combinations ranked in the order of what we a priori believed would be the least to most favourable habitat for carabids: –refuge/+insecticide, –refuge/–insecticide, +refuge/+insecticide and +refuge/–insecticide. Significance of the correlations was tested by a Spearman test (PROC CORR; SAS Institute 1996).

Results

A total of 2128 adult beetles representing 33 species was collected in 1998, and 3234 adult beetles representing 37 species were collected in 1999 (Table 1). *Pterostichus melanarius* (Ill.) was the dominant species of both years, comprising 29·4% and 53·2% of total captures in 1998 and 1999, respectively.

ACTIVITY DENSITY IN THE STRIP AND CROP AREA

To illustrate general trends in the entire plot, carabids captured in strips and crop areas were combined (Fig. 2a,b). Before planting corn in 1998, the numbers

Table 1. Number of carabid beetles captured by species and percentage of total captured in the study from April to October 1998 and March to September 1999, Michigan State University Entomology farm, Michigan, USA

Species	1998		1999	
	Number	% total	Number	% total
Pterostichus melanarius (Ill.)	624	29·4	1722	53·2
Poecilus lucublandus (Say)	264	12·4	468	14·5
Amara aenea (DeG.)	226	10·6	135	4·2
Pterostichus permundus (Say)	141	6·6	94	2·9
Clivina impressifrons LeC.	140	6·5	154	4·8
Bembidion quadrimaculatum Say	110	5·2	59	1·8
Poecilus chalcites (Say)	88	4·1	34	1·1
Anisodactylus sanctaecrucis (F.)	86	4·0	38	1·2
Stenolophus comma (F.)	81	3·8	11	0·3
Agonum cupripenne (Say)	65	3·1	3	0·09
Elaphropus anceps (LeC.)	62	2·9	118	3·6
Harpalus herbivagus (Say)	46	2·2	17	0·5
Cyclotrachelus sodalis (LeC.)	25	1·2	71	2·2
Harpalus pensylvanicus (DeG.)	12	0·6	81	2·5
Other species (19 spp.; 23 spp.)	158	7·3	229	7·1
Total	2128		3234	

of carabid beetles captured in the entire plot were similar among treatments (Fig. 2a). Before planting in 1999, overall activity density was generally high in treatments with refuges (Fig. 2b). After planting, captures of carabids dropped in both years in plots where insecticide was applied. During the summer–autumn, carabid activity density remained low in –refuge/+insecticide plots, whereas activity density increased in +refuge/+insecticide plots. The two sampling areas, strips and crop areas, had different sampling efforts and treatments applied and thus, for the remainder of

the paper, activity density within the strips and crop areas will be presented separately.

First year of study (1998)

Before planting, activity density in the strips was not significantly different among the four treatments (Fig. 3a). Likewise, activity density in crop areas was not significantly different (Fig. 3a), suggesting the field was relatively homogeneous in beetle activity prior to major experimental manipulation. Insecticide had
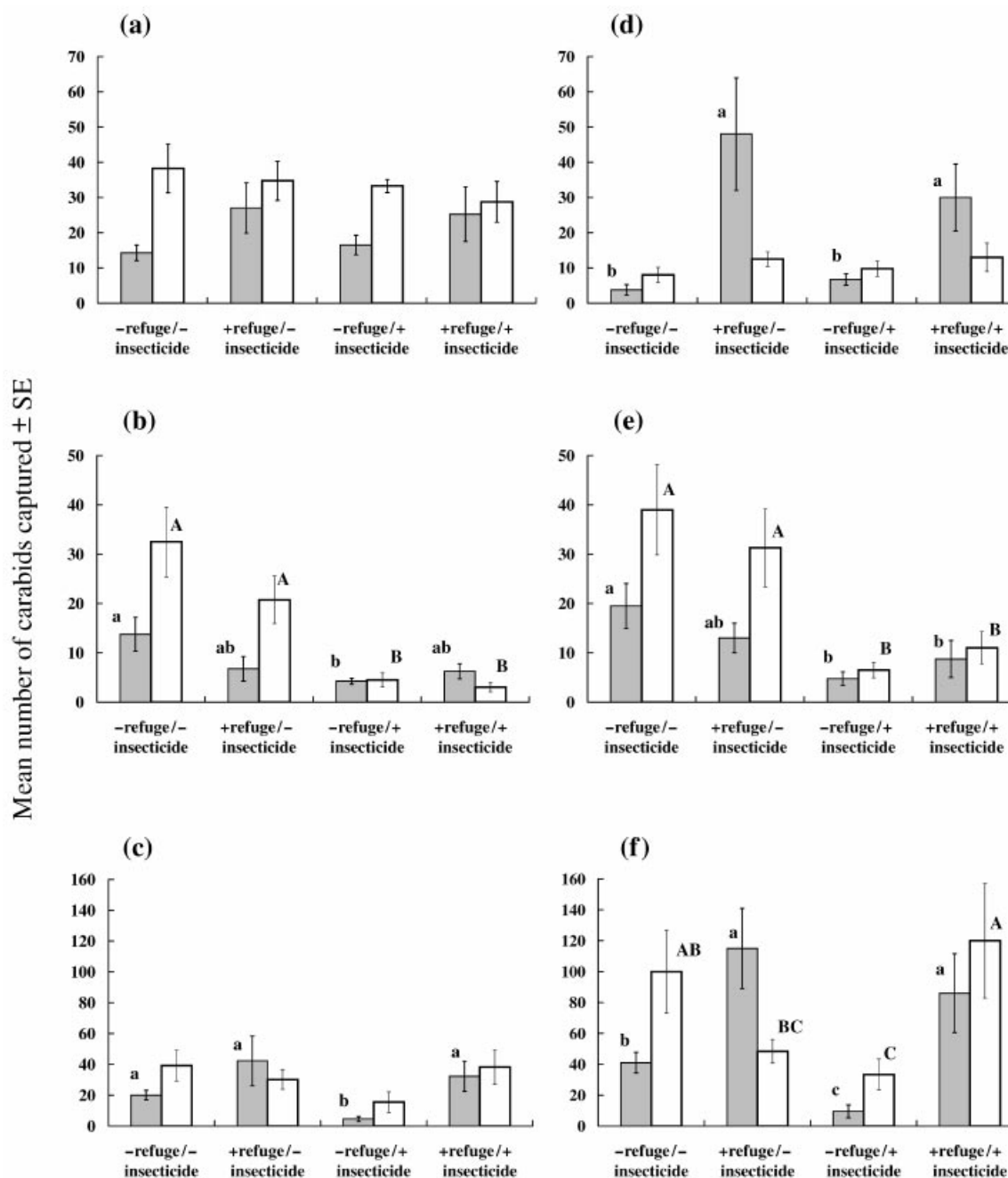

Fig. 3. Mean activity density of carabids ± SE in the strip (■) and crop (□) areas in 1998 and 1999. Different letters denote significant differences based on LSD of square-root transformed data, *P* < 0·05. Lower case letters compare refuge and –refuge strips and capitalized letters compare crop areas of the four treatments. (a) Before planting 1998; (b) after planting 1998; (c) summer–autumn 1998; (d) before planting 1999; (e) after planting 1999; (f) summer–autumn 1999.

Table 2. Analysis of variance for activity density of carabid beetles in the strip and crop areas in 1998 and 1999, Michigan State University Entomology farm, Michigan, USA

Area	Time period	Sources of variation	d.f.	1998 F	1998 P	1999 F	1999 P
Refuge or –refuge strip	Before planting	Refuge	1,3	1·76	0·28	32·6	0·01
		Insecticide	1,6	0·01	0·94	0·3	0·60
		Refuge × insecticide	1,6	0·45	0·53	2·47	0·17
	After planting	Refuge	1,3	1·06	0·38	0·02	0·90
		Insecticide	1,6	3·18	0·12	13·7	0·01
		Refuge × insecticide	1,6	3·7	0·10	3·52	0·11
	Summer–autumn	Refuge	1,3	7·0	0·08	51·8	0·006
		Insecticide	1,6	5·83	0·05	34·3	0·001
		Refuge × insecticide	1,6	1·61	0·25	5·3	0·06
Crop area	Before planting	Refuge	1,3	0·3	0·62	1·05	0·38
		Insecticide	1,6	2·9	0·14	0	0·99
		Refuge × insecticide	1,6	0·19	0·68	0·8	0·41
	After planting	Refuge	1,3	2·55	0·21	0	0·99
		Insecticide	1,6	45·9	0·0005	25·8	0·002
		Refuge × insecticide	1,6	0·73	0·43	1·28	0·30
	Summer–autumn	Refuge	1,3	0·73	0·46	1·64	0·29
		Insecticide	1,6	1·07	0·34	0·09	0·77
		Refuge × insecticide	1,6	2·35	0·18	20·3	0·004

not yet been applied and barriers were not yet present to limit movement.

After planting, activity density in strips of –refuge/ –insecticide plots appeared to be higher than strips of –refuge/+insecticide plots (Fig. 3b). As refuge × insecticide interactions marginally impacted activity density in the strips ($P = 0.1$; Table 2), multiple comparisons of the four treatments shown in Fig. 3b should be viewed with caution. In the crop area, significantly fewer carabids were captured in insecticide-treated than untreated crop areas (Table 2 and Fig. 3b).

During the summer–autumn of 1998, prior insecticide use in the adjacent crop area impacted activity density within strips (Table 2). Strips of –refuge/+insecticide plots had significantly lower activity density than strips of the other three treatments (Fig. 3c). Crop areas within –refuge/+insecticide plots appeared to have lower activity density than the other three treatments but differences were not significant (Fig. 3c).

Second year of study (1999)

Before planting, refuge strips had significantly higher activity density of beetles than –refuge strips (Table 2 and Fig. 3d). However, activity density in crop areas was not different among treatments, regardless of the presence of an adjacent refuge or previous insecticide use (Fig. 3d). This result suggests that, in early spring, refuges augmented beetles within the refuge but not within the adjacent crop area.

After planting, insecticide application in the adjacent crop area significantly impacted activity density within strips (Table 2). –Refuge strips adjacent to untreated crop areas had higher activity density than strips adjacent to insecticide-treated crop areas (Fig. 3e). In

the crop area, activity density was significantly lower within insecticide-treated crop than untreated crop areas (Table 2 and Fig. 3e).

During summer–autumn, both the presence of a refuge and prior insecticide use in the adjacent crop area impacted activity density within strips (Table 2). Refuge strips had higher activity density than –refuge strips (Fig. 3f). Refuge × insecticide interactions affected activity density in crop areas (Table 2). Captures within crop areas of +refuge/+insecticide and –refuge/ –insecticide plots were significantly higher than –refuge/ +insecticide plots (Fig. 3f). Crop area captures in +refuge/+insecticide plots were significantly higher than in +refuge/–insecticide plots. Interestingly, as insecticide toxicity declined, captures in treated crop areas adjacent to refuges surpassed those adjacent to –refuge strips. This suggests that, compared with insecticide-free crop strips, refuges were an important source of beetles that colonized the adjacent crop areas previously perturbed by insecticide. Although +refuge/–insecticide plots had high overall activity density, many beetles were captured in the refuge and not in the crop area (Fig. 3f). Therefore, refuges did not appear to augment carabids in undisturbed crop areas.

SPECIES RICHNESS AND COMMUNITY COMPOSITION IN THE CROP AREA

The number of species appeared to be lower in crop areas treated with insecticide after planting in 1998 and 1999 (Table 3). However, when species richness was adjusted for sample size, treatments were not significantly different during any of the time periods.

Carabid community composition in the crop area was similar across all treatments before planting in

Table 3. Mean number of carabid species, sample size and species richness (Menhinick index) ± SE in the crop area during 1998 and 1999, Michigan State University Entomology farm, Michigan, USA

Time period	Treatment	Number of species	Sample size	Species richness
Before planting 1998	– refuge/–insecticide	11·8 + 0·63	38·3 + 6·9	1·96 + 0·11
	+refuge/–insecticide	11·0 + 1·22	34·8 + 5·5	1·91 + 0·23
	– refuge/+insecticide	10·5 + 0·87	33·3 + 1·9	1·83 + 0·15
	+refuge/+insecticide	10·5 + 1·44	28·8 + 5·8	1·99 + 0·14
Before planting 1999	– refuge/–insecticide	4·0 + 1·1	8·0 + 2·1	1·38 + 0·28
	+refuge/–insecticide	6·0 + 0·7	12·5 + 2·1	1·74 + 0·18
	–refuge/+insecticide	4·0 + 1·1	9·8 + 2·1	1·25 + 0·23
	+refuge/+insecticide	6·3 + 1·8	13·0 + 4·1	1·72 + 0·32
After planting 1998	– refuge/–insecticide	7·8 + 0·9	32·5 + 7·1	1·39 + 0·12
	+refuge/–insecticide	6·5 + 1·0	20·8 + 4·8	1·44 + 0·09
	–refuge/+insecticide	3·5 + 1·2	4·5 + 1·4	1·57 + 0·34
	+refuge/+insecticide	2·3 + 0·5	3·0 + 0·9	1·31 + 0·11
After planting 1999	– refuge/–insecticide	6·8 + 1·0	39·3 + 9·2	1·1 + 0·04
	+refuge/–insecticide	7·3 + 0·5	31·3 + 7·9	1·43 + 0·27
	–refuge/+insecticide	3·5 + 0·1	6·5 + 1·6	1·41 + 0·18
	+refuge/+insecticide	4·0 + 0	10·8 + 3·3	1·38 + 0·24
Summer–autumn 1998	– refuge/–insecticide	6·3 + 0·6	39·3 + 10·0	1·07 + 0·13
	+refuge/–insecticide	7·5 + 0·5	30·3 + 6·3	1·45 + 0·23
	–refuge/+insecticide	4·0 + 1·4	15·5 + 6·7	1·21 + 0·08
	+refuge/+insecticide	8·0 + 1·7	30·8 + 7·8	1·55 + 0·28
Summer–autumn 1999	– refuge/–insecticide	9·0 + 1·0	100·3 + 26·8	0·97 + 0·13
	+refuge/–insecticide	9·0 + 1·3	48·3 + 7·7	1·3 + 0·09
	–refuge/+insecticide	7·5 + 1·2	33·3 + 10·1	1·46 + 0·28
	+refuge/+insecticide	9·3 + 0·9	119·8 + 37·1	0·94 + 0·17

1998. Plots of all four treatments were scattered about the DCA ordination graph (Fig. 4a), and DCA axis scores were not significantly correlated with any variables. After planting in 1998, DCA axis 2 scores correlated negatively with refuge × insecticide combinations ($r = -0.498$, $P = 0.05$). Plots with refuge × insecticide combinations considered least favourable for carabids were situated higher on the graph, –refuge/+insecticide plots being situated highest on the graph (Fig. 4b). During the summer–autumn in 1998, communities remained affected by prior insecticide use, as indicated by DCA axis 1 scores being correlated positively with insecticide use ($r = 0.866$, $P = 0.001$). Plots treated with insecticide were present on the right side of the graph, while plots without insecticide inputs were on the left side (Fig. 4c).

In 1999 before planting, the presence of an adjacent refuge impacted community composition within the crop area. DCA axis 2 scores correlated positively with refuge ($r = 0.488$, $P = 0.05$) and plots with refuges were on the upper part of the graph (Fig. 4d). Immediately following planting, insecticide changed carabid communities. Insecticide use correlated positively with DCA axis 1 scores ($r = 0.841$, $P = 0.0001$), with insecticide-treated plots situated on the right of the graph and untreated plots situated on the left (Fig. 4e). During the summer–autumn of 1999, DCA axis 2 scores correlated positively with insecticide use ($r = 0.624$, $P = 0.01$). In addition, DCA axis 2 scores correlated negatively with refuge × insecticide combinations ($r = -0.643$, $P = 0.007$). Treatments with refuge × insecticide combinations considered less favourable for carabids were on the upper part of the graph. Notably, +refuge/+insecticide plots

were no longer clustered with –refuge/+insecticide plots and were closer to plots without insecticide. Meanwhile –refuge/+insecticide plots were separated from the rest of the plots (Fig. 4f).

Discussion

Insecticide application represented an intense ecological disturbance on carabids, as evidenced by their decrease in activity density and shifted community composition in crop areas. Although terbufos persists in the soil for approximately 3 weeks or longer (Harris 1977; Lesiewicz, Van Duyn & Bradley 1984), it may have season-long effects. As terbufos is highly toxic to carabid larvae (Tomlin 1975), few adults would be expected to emerge in the following summer months. In this study, insecticide-treated crop areas without an adjacent refuge had very low activity density throughout summer–autumn. The few adults captured in these plots probably developed as larvae in the insecticide-free –refuge strip.

Refuges had a strong impact on carabid assemblages. Before planting in 1999, refuges had very high carabid activity density. As seen in other studies, refuges harbour many active beetles early in the season (Thomas, Wratten & Sotherton 1991; Carmona & Landis 1999). Some species of carabids are known to overwinter in field boundaries (Sotherton 1984, 1985; Thomas, Wratten & Sotherton 1992), thus high captures observed in our refuges before planting in 1999 may be due to carabids emerging from their overwintering site. Also, dense vegetation in the refuge may
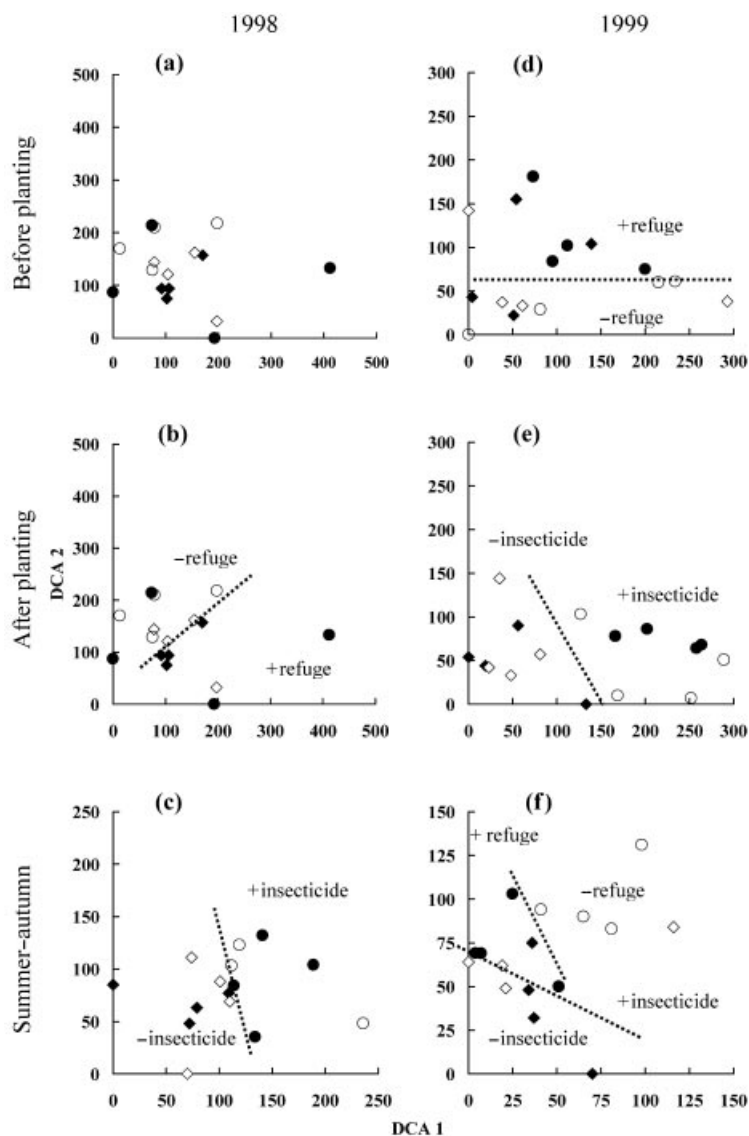
1998   1999

Fig. 4. DCA ordination of carabid communities in the crop area of –refuge/–insecticide (◇), +refuge/–insecticide (◆), –refuge/+insecticide (○) and +refuge/+insecticide (●). (a) Before planting 1998; (b) after planting 1998; (c) summer–autumn 1998; (d) before planting 1999; (e) after planting 1999; (f) summer–autumn 1999. Lines demarcating trends are shown.

create a more favourable microclimate (Chiverton & Sotherton 1991). As a result, more carabids would be expected to aggregate in a refuge as opposed to a bare field. Before planting in 1998, carabids were not heavily aggregated in the refuge and two factors may explain the observed results. First, sampling in 1998 started later and carabids may have already dispersed into the field. Secondly, barriers were not present in 1998 as in 1999, and carabids from other sites may have also been dispersing into the field.

In terms of biological control, the impact that refuges have on adjacent fields is of great significance. Refuges may protect populations from disturbances (Kareiva 1990) and serve as a source of natural enemies to disturbed areas. Wissinger (1997) pointed out that some natural enemies, including carabids, require stable overwintering habitats but could later colonize ephemeral sites such as annual crops during favourable

periods. When the quality of ephemeral habitats declines, these natural enemies should return to the permanent habitat following a 'cyclic colonization' pattern. Previous studies have documented that carabids disperse between habitats of various stability (Duelli *et al.* 1990; Kajak & Lukasiewicz 1994) and that fields with refuges have more carabids than fields without refuges (Hassall *et al.* 1992; Lys & Nentwig 1992; Lys, Zimmerman & Nentwig 1994). Also, the abundance of carabids in a refuge has been correlated positively with carabid abundance in the field (Coombes & Sotherton 1986; Hawthorne & Hassall 1995). Furthermore, carabid activity density decreases as distance from the refuge source increases, providing evidence that beetles disperse from refuges into fields (Coombes & Sotherton 1986; Thomas, Wratten & Sotherton 1991; Dennis & Fry 1992; Vitanza, Sorenson & Bailey 1996).

Our study corroborates previous findings by

demonstrating directly that refuges can contribute to greater carabid populations in the field. In the past, it has been difficult to determine conclusively whether beetles found in the field originated from the refuge habitat, as carabids can be quite mobile. Radar tracking studies indicate a net displacement of 5·3 m day^{-1} (Wallin & Ekbom 1988), and mark and recapture studies indicate movement of 0·4–58 m day^{-1} (Lys & Nentwig 1991). Knowing these challenges, we controlled possible carabid movement with plastic barriers. Under these experimental conditions, beetles that appeared in insecticide-treated crop areas in summer–autumn probably dispersed from the refuge or –refuge strip as terbufos depleted the previously existing carabid population. As seen in the second year, refuges were an important source of carabids for disturbed fields, increasing activity density in adjacent treated crop areas. In previous studies, carabid beetles have been observed to recolonize an insecticide-disturbed field from the edges towards the centre, but the source of colonizing carabids was not from refuge habitats (Jepson & Thacker 1990) as found in this study, or was not investigated (Duffield & Aebischer 1994).

In addition to affecting carabid activity density, refuge habitats may impact the carabid community composition. Species richness of carabids has been observed to decline as distance from refuges increases (Fournier & Loreau 1999). Frank (1997) found that fields with newly sown refuges increased in carabid species richness from the first to second year of refuge establishment. Our study compared directly effects of refuge vs. crop vegetation on carabids and did not find evidence that the refuge impacted species richness in the crop area, but did find evidence that refuges impacted community composition. Carabid communities among several agricultural habitats have been evaluated and found to differ within various types of refuge vegetation and within crop fields (Asteraki, Hanks & Clements 1992, 1995). Also, carabid communities within insecticide-disturbed rangelands have been observed to return to their pre-disturbed state quickly when certain ground vegetation was present (Quinn *et al.* 1991). Given the importance of vegetative habitats on carabid communities, our study specifically addressed how discrete refuge vegetation would impact carabid communities in adjacent agricultural fields. In 1999, communities within insecticide-treated crop areas clearly separated from communities within untreated crop areas following planting. But during summer–autumn, communities within crop areas of +refuge/+insecticide plots no longer clearly clustered with –refuge/+insecticide plots and became similar to communities within untreated crop areas. Although insecticide altered community composition, the presence of a refuge had a buffering effect such that communities in disturbed crop areas gradually came to resemble communities not subjected to insecticide disturbance.

The interactions between refuge and adjacent crop areas were not always straightforward. As seen during summer–autumn in 1999, many carabid beetles were captured in +refuge/–insecticide plots but most were captured within refuge strips. Contrary to our expectations, the activity density of carabids was not higher in crop areas of +refuge/–insecticide plots than –refuge/+insecticide plots. We suggest three possible reasons for the unanticipated outcome.

First, although enclosures were necessary to demonstrate that refuges were a source of carabids colonizing the crop, they may have unknown consequences on foraging behaviour and competition of carabids. The 15×15-m enclosures used in this study were larger than those used in previous studies that attempted to maintain carabids within an area (Edwards, Sunderland & George 1979; Chiverton 1987; Frampton *et al.* 1995; Mauremooto *et al.* 1995; Menalled, Lee & Landis 1999). Carabids that dispersed from refuges in our experimental plots may have been more likely to return to the refuge because they encountered a barrier to movement. Nevertheless, as all treatments had the same plot size and barrier design, any potential impact that barriers may have had on carabid behaviour should not have biased our results.

Secondly, while refuges conserve carabid beetles (Thomas, Wratten & Sotherton 1992), under certain conditions refuges may also retain beetles, acting as a 'sink' (Corbett & Plant 1993), or may be a barrier to movement (Frampton *et al.* 1995; Mauremooto *et al.* 1995). Yet in our study, crop areas that were treated with insecticide and adjacent to refuge strips had high carabid captures. This result suggests that, although refuges enhance overall carabid abundance, there is an interaction between refuge habitats and insecticides that determines the net movement of carabids between refuges and crop fields.

Thirdly, even though soil insecticide application clearly decreased habitat quality for carabids in the short term, it may have altered (decreased or increased) prey fauna, causing a rise in activity density of carabids in the long term. If terbufos reduced the long-term availability of prey, high rates of carabid captures in the crop areas could be due to an increase in activity of hungry carabids. For example, Chiverton (1984) found that, after a recovery period, carabids were more active in insecticide-treated areas due to lower food availability. Starved beetles tend to move faster and greater distances (Wheater 1991; Frampton *et al.* 1995; Mauremooto *et al.* 1995). However, observations made in our field with marked and recaptured beetles did not indicate beetles to be more active in insecticide-treated plots. The number of carabids recaptured during a sampling period vs. the total number marked for the treatments –refuge/–insecticide, +refuge/–insecticide, –refuge/+insecticide, and +refuge/+insecticide were 22/148, 27/199, 5/28 and 27/212, respectively (J. C. Lee, unpublished data). While terbufos might be expected to reduce food resources, terbufos may, on the other hand, increase prey availability in crop areas for the long term. When insecticide inputs eliminate early season predators,

certain prey can thrive and become very abundant once toxicity levels have declined (Menhinick 1962). Therefore, the abundance of prey and chemical cues emanating from prey may attract or retain more beetles in the crop area (Wheater 1989; Kielty *et al.* 1996). Consequently, while refuges harbour many carabids, more carabids might eventually be drawn into insecticide-treated crop areas than untreated crop areas.

Conclusion

Over this 2-year study, insecticide application generated a disturbance, reducing carabid activity density and altering community composition in the field. As hypothesized, in the second year, the refuge ameliorated the negative effects by providing a source of colonizing beetles increasing carabid activity density in the field, thereby influencing community composition. Yet, refuges did not consistently augment beetles in adjacent crop areas that were not disrupted with insecticide. Thus, future work should address the mechanisms that govern carabid dispersal and retention among refuge and crop habitats at the farm scale. Carabids are long-lived predators, highly susceptible to broad-spectrum insecticides, and, consequently, pest populations normally controlled by carabids would increase after insecticide application (Trumper & Holt 1998). However, using refuge habitats to augment predatory carabids in cornfields during midsummer may help maintain aphids (Hance 1990), leafhoppers and thrips (Lang, Filsner & Henschel 1999) and sporadic pests such as black cutworm *Agrotis ipsilon* (Hufnagel) (Lund & Turpin 1977b) and armyworm *Pseudelatia unipuncta* (Haworth) (Clark *et al.* 1994) at low levels. Given that refuge habitats also benefit many other predators such as staphylinids and arachnids, refuge habitats can have a very important role in maintaining general natural enemy populations in disturbed agricultural fields (Boller, Redmund & Candolfi 1988; Thomas, Wratten & Sotherton 1992; Halley, Thomas & Jepson 1996; Lester, Thistlewood & Harmsen 1998). Our study demonstrates the importance of refuge habitats as a reservoir of natural enemies that is critical for successful biological control of pests in otherwise unstable annual crop habitats (Wiedenmann & Smith 1997; Wissinger 1997).

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