Movement Patterns of Carabid Beetles Between Heterogenous Crop and Noncrop Habitats

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Abstract

Habitats adjacent to crop fields can increase natural enemy populations by providing additional food, shelter and overwintering sites. While many studies have focused on the role of non-crop borders for supporting natural enemies, here we investigate the influence of adjacent crop habitats as well. We monitored the movement of carabid beetles (Coleoptera: Carabidae) between wheat fields and adjacent crop and non-crop habitats using bi-directional pitfall traps. We found greater movement of carabids from corn into wheat fields than from forest and soybean, with intermediate levels of movement from roadside vegetation. Additionally, significantly more carabids were captured moving into corn from wheat than into any other habitat. We also found that carabid community assemblages at habitat borders were different from those in the interior of wheat fields. Our findings suggest that agricultural ecosystems composed of a variety of both non-crop and crop habitats are necessary to maintain carabid abundance and diversity.

Permanent and semi-permanent non-crop habitats surrounding agricultural fields, like grassy strips, hedgerows, woodlots, and grasslands are important for conservation biocontrol. These habitats harbor increased diversity of natural enemies of pests by providing additional food resources, shelter and overwintering sites (Varchola and Dunn 2001, Landis et al. 2005). Due to pest outbreaks during the summer, field crops may at times contain a high availability of food and encourage the movement of predators into crops where competition for prey is low (Wallin and Ekbom 1988). Natural enemies may colonize crops under such conditions, but retreat back to non-crop habitats once the crops have become unsuitable to live in (i.e., after harvest or pesticide application) (French et al. 2004, Landis et al. 2005, Gavish-Regev et al. 2008). Such movement back and forth between crops and non-crop habitat may be important for natural enemy efficacy (Wissinger 1997, Tscharntke et al. 2008).

One group of natural enemies that exhibits this movement between various habitats is the carabid beetles (Coleoptera: Carabidae). These polyphagous beetles can consume an amount of food nearly equivalent to their body mass each day (Lindroth 1961-1969, Kromp 1999). Carabid beetles typically forage for prey at the soil surface (Lindroth 1961-1969), however, certain species will occasionally forage below the surface (Lee and Edwards 2012) or climb plants (Lovei and Szentkiralyi 1984, Sasakawa 2010) in search of seeds or insects. Carabids are important generalist predators in agricultural systems because they feed on known crop pests such as aphids (Sunderland et al. 1987, Winder et al. 2005, Hajek et al. 2007), slugs (Bohan et al. 2000, Eskelson et al. 2011, Hatteland et al. 2011), and weed seeds (Gallandt et al. 2005, White et al. 2007, Bohan et al. 2011). Studies have shown that higher abundances of carabids in

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crop fields lead to lower pest populations (Lang 2003, Bohan et al. 2011, Lee and Edwards 2012).

Carabid diversity and abundance are influenced by habitats surrounding agricultural fields at various scales. At the local field scale, many studies have found that more complex habitats with higher plant diversity and more cover support higher carabid abundance and species diversity than more simple habitats with lower plant diversity and/or less cover (Asteraki et al. 1995, Shearin et al. 2008, Taboada et al. 2010, Blubaugh et al. 2011). In addition, carabid beetle abundance and diversity are affected at the landscape level, which consists of a mosaic of various crop fields and non-crop habitats. Bommarco (1998) found that the amount of field edge and the presence of non-crop habitats in an agricultural landscape may even affect fecundity and adult body size of carabids. At this scale, non-crop habitats may act as dispersal corridors for carabids and affect carabid assemblages at distances of up to one kilometer (Burel 1989). As such, agricultural landscapes with greater habitat diversity and more non-crop habitat harbor greater carabid diversity and abundances (Weibull et al. 2003, Schweiger et al. 2005, Werling and Gratton 2008).

Studies examining the movement of carabid beetles between habitats in agroecosystems have often focused on the role of border habitats like hedgerows and grassy banks as barriers to movement between fields (Frampton et al. 1995, Mauremooto et al. 1995, Holland et al. 2004, 2005). The potential role of other crop habitats, as opposed to non-crop habitats, in supplying natural enemies to crop fields has been largely overlooked, despite the fact that different crop habitats may provide complementary food and shelter resources (Vasseur et al. 2013). In this study, we explicitly examined different types of habitat commonly found adjacent to wheat fields in Michigan to determine their relative importance for providing carabid beetles to wheat fields. We studied the movement of carabids between wheat fields and two crop habitats (corn and soybean) as well as two non-crop habitats (forest and grassy-roadside vegetation) and quantified carabid activity-density and community assemblages.

Materials and Methods

Study Site. This study was conducted in Gratiot County, MI in a landscape dominated by field crop production. Crops grown in this region primarily consist of corn, soybean and wheat, with smaller proportions of sugar beets and alfalfa. Non-crop habitats in this region primarily consist of fencerows, woodlots on marginal lands, and grassy roadside margins. The fields in this study were managed in a conventional corn – soybean – wheat rotation. Data were collected in four wheat fields surrounded by typical crop and non-crop vegetation of the region (Table 1). We sampled carabid beetles along multiple border types in each field, using methods modified from Vasseur (2012). The four wheat fields used in this study were planted in autumn of 2010 and harvested 13-21 July 2011.

Carabid monitoring. We monitored carabid movement using pitfall traps consisting of 0.95 L cups (Fabri-Kal, Kalamazoo, MI) buried flush with the soil surface and filled with 2 cm of 50:50 propylene glycol: water mixture (Fig. 1A). Squares of 0.6 cm mesh-hardware cloth (10 cm x 10 cm) were placed into each cup, 2 cm from the top to prevent the capture of mammals and amphibians. Plastic plant saucers (20 cm diameter) were inverted and suspended over each cup using 3 pin flags to prevent overflow during rainfall. In each station, two identical cups were placed 10-20 cm apart. Pitfall traps were used continuously in wheat field centers and borders from 23 May 2011 through 21 June 2011. Samples were stored in 70% ethanol and all carabids were identified to species using a reference collection from the Michigan State University Department of Entomology Albert J. Cook Arthropod Research Collection, as well as reference to an identification guide (Lindroth 1961-1969).

Table 1. Size, coordinates, and number of bi-directional traps per adjacent habitat for each wheat field used in surveys of carabid beetle abundance and species composition.

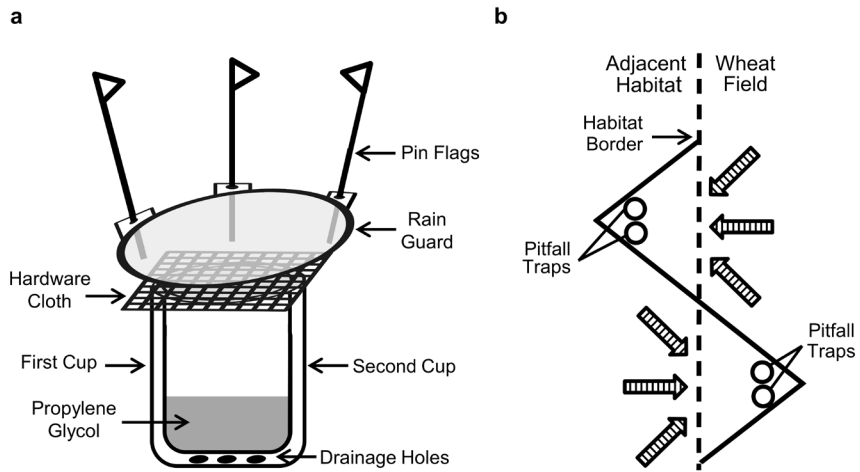| Field	Size (ha)	Coordinates	# of traps in each habitat				Total traps/ field
			Corn	Forest	Roadside	Soybean	
A	20	43 23' 15.51" N 84 46' 55.04" W	2	5	1	0	8
B	36	43 22' 07.80" N 84 47' 01.96" W	2	2	2	2	8
C	26	43 19' 49.71" N 84 46' 57.69" W	3	2	1	2	8
D	15	43 17' 15.17" N 84 37' 47.44" W	3	2	0	0	5
Total traps/ habitat			10	11	4	4	29

Figure 1. Pitfall (a) and bidirectional Z (b) trap designs. In panel (b), dashed arrows indicate carabid movement between a wheat field and an adjacent habitat. Habitats that carabids exited (beginning of the arrows) are referred to as source habitats. Habitats that carabids entered (apex of the arrows) are referred to as destination habitats.

Carabid movement between wheat fields and surrounding habitats was monitored using bidirectional traps placed at field edges (Fig. 1B; Vasseur 2012). Traps were constructed of corrugated plastic sheets, measuring 60 cm tall and 4 mm thick, stapled together to form a Z shape. The shorter arms of the Z were 1 m long and attached at right angles to the longer portion, which measured 1.5 m. The traps were placed so that one apex of the Z enclosed wheat and the other apex enclosed an adjacent habitat. Traps were buried 15-20 cm in the soil and two pitfall traps (Fig. 1A) were placed in each apex of the Z. Because the pitfalls were placed 1 meter into the other habitat type, carabid beetles had ample time to turn around and return to the source habitat if conditions were not suitable in the destination habitat. In this way, Z traps indicate carabid beetles' initial preference for a given habitat.

Each field had 5-8 bidirectional Z traps to intercept carabids moving between wheat and corn, soybean, forest, or roadside habitats (Table 1). Traps were distributed among habitat types proportionally to the amount of each habitat bordering a given wheat field. For example, if a wheat field shared approximately 25% of its perimeter with corn, then 2 of the 8 border traps were placed at corn-wheat edges. The traps for each border type were spread out in different cardinal directions whenever possible to account for possible cardinal direction biases in carabid movements. Carabid activity-density within the fields was monitored with sampling stations placed in the interior of wheat fields 130-175 m apart. These stations consisted of two standard pitfall traps placed 20 cm apart. Each field contained 4 of these interior sampling stations, except for field D which only contained 3, for a total of 15 interior stations.

Statistical Analyses.

Contributions of Source Habitats and Preference for Alternate Habitats. To measure the relative contributions of different source habitats (corn, forest, roadside vegetation and soybean) to carabid activity-density within wheat fields, we used trap captures for carabids moving into wheat from each adjacent habitat type (i.e., source habitats). To measure carabid preference for different adjacent habitats (i.e., destination habitats), we used trap captures for carabids

moving from wheat into each adjacent habitat type. Any samples that were compromised due to flooding or tampering by mammals were removed prior to analysis. For these two separate comparisons, we determined the mean number of carabids per trap in each habitat and compared these means using one-way analyses of variance (ANOVA; Proc GLIMMIX, SAS 9.2, SAS Institute, 2009) followed by Tukey-Kramer post hoc tests. Mean trap captures were square-root transformed prior to analysis to help normalize variance. Edge habitat type was included as the fixed effect and site was included as a random variable. Weekly activity-density data were included as replicate samples after initial analyses indicated no effect of week on carabid captures.

Carabid Community Assemblage. To compare carabid community assemblages (i.e., the species present and their relative activity-densities) among the habitats, a Bray-Curtis Similarity Index was calculated for each pair of pitfall trap locations. Traps in wheat field centers were used to describe communities in wheat, and trap captures of carabids moving into wheat were used to describe community composition of carabids being supplied by each of those habitats. The BC Index is a similarity index ranging from 0-100, with 0 representing communities that are completely dissimilar (have no species in common), and 100 representing communities that are completely similar (have all the same species in the exact same abundances). The following is the equation for the index, where p is the number of species, Y is the number of individuals of species i in a given sample, and j and k represent any two sample units:

$$S_{jk} = 100 * \{1 - \frac{\sum_{i=1}^{p} |Y_{ij} - Y_{ik}|}{\sum_{i=1}^{p} (Y_{ij} - Y_{ik})}\}$$

Because larger populations tend to have higher variances over time, the activity-density in a single sample may not be an accurate estimate of the average activity-density of that species over time. Thus, it is important to avoid strong influences of high activity-density of common species on relative similarity calculations (Clarke and Warwick 2001). To do this, the total number of individuals per species in each trap was averaged across the 5 weekly samples and then square root transformed. Species comprising less than 1% of total carabid capture were also excluded from analysis to avoid disproportionate influences of rare species on similarity calculations.

To compare community similarity across habitats, an Analysis of Similarity (ANOSIM) was conducted in Primer Primer 6.0 (Primer-E Ltd, Ivybridge, UK) on the rank similarities of each sample pair. Here, the measure of the effect of habitat on similarity between samples is calculated by the R test statistic, which is similar to an F statistic in an ANOVA. The R test works with the null hypothesis that habitat type does not affect the similarity between traps, meaning that random switching of the habitat assigned to each sample would have no effect on similarity. In ANOSIM, the habitat labels for each trap are randomly reassigned and a new R statistic is calculated to measure the effect of habitat on sample similarity. This was repeated 999 times for each pair of habitats, except for the roadside-soybean pair, which was permuted 495 times because there were fewer soybean trap samples. The probability that the R value from the data indicates a significant difference between habitats is equal to the number of times that an R value of equal or greater value is generated by chance during the random reassignments, divided by the total number of random reassignments. To avoid the confounding effects of multiple comparisons on significance, we adjusted α-values accordingly using the Benjamini and Hochberg False Discovery Rate Control (FDR) Procedure (Verhoeven et al. 2005).

Results

A total of 1398 adult carabid beetles comprising 37 species were collected during the 5 weeks of this study. Seven species of carabid beetles each contributed 5% or more of total captures: *Pterostichus melanarius* (Ill.)*, Amara aenea* (DeGeer)*, Agonum placidum* (Say)*, Poecilus lucublandus* (Say)*, Harpalus herbivagus* (Say)*, Chlaenius tricolor* (Dejean) *and Poecilus chalcites* (Say) (Table 2).

Relative contributions of source habitats. Overall, source habitat significantly influenced activity-density of carabids entering wheat fields ($F = 12.05$; df = 3, 239; $P < 0.0001$; Fig. 2). Corn fields contributed significantly more carabids to wheat fields than forest ($t = 5.80$; $P < 0.0001$) and soybean ($t = 2.94$; $P = 0.0185$), but not roadside vegetation ($t = 2.14$; $P = 0.1433$). There were no significantly different contributions between any of the remaining habitats. The most commonly captured species entering wheat fields from each border habitat type are shown in Table 3.

Carabid preference for alternate habitat types. Overall, destination habitat had an effect on carabid movement ($F = 10.12$; df = 3, 239; $P < 0.0001$; Fig. 2). There were significantly more carabids moving from wheat into corn than from wheat into forest ($t = 4.71$; $P < 0.0001$), roadside vegetation ($t = 4.19$; $P = 0.0002$) or soybean ($t = 2.91$; $P = 0.0203$). There were no significant differences of carabid preference among forest, roadside, or soybean vegetation. The most commonly captured species leaving wheat fields at each border habitat type are shown in Table 3.

Community assemblages. Overall, carabid community assemblages varied among all habitats ($R = 0.244$; $P = 0.01$). In pairwise comparisons, communities in all habitats were significantly differently from one another, except those in roadside vegetation versus corn and roadside vegetation versus forest (Table 4). Carabid communities in each habitat differed in abundant species and the relative activity-density of these species (Fig. 3). The following results compare only corn, roadside, forest, and wheat, due to low captures in soybean. Considering the four most captured species in each habitat, *Am. aenea* was among among the most captured species in all four habitats, while *Pt. melanarius* was amont the most captured in all habitats but forest, and *H. herbivagus* in all habitats but wheat. *Ag. placidum* was among the top four most captured species in wheat and roadside habitats and *Ch. tricolor* was among the most captured species in wheat and forest habitats. *Po. lucublandus* was among the most captured species in corn only and *Anisodactylus rusticus* (Say) was among the most captured species only in the forest habitat.

Discussion

The carabid communities represented in this study show similarities and differences to carabid communities identified in previous studies in this region. Of the seven carabid species with the highest activity-density in this study, *Pt. melanarius* and *Po. lucublandus* were also among the most captured in three other studies examining carabid activity in Michigan agricultural habitats, while four other species were among the most captured in at least one of the earlier studies (Clark et al. 1997, Carmona and Landis 1999, Lee et al. 2001). However, *Ch. tricolor*, which made up more than 7% of our captures, made up less than 1% of captures in the previous studies. Additionally, some species that were among the most captured in the earlier studies were captured in low densities (e.g., *Pt. permundus* (Say), *H. pennsylvanicus* (DeGeer), *Bembidion quadrimaculatum* (Say), and *Ag. cupripenne* (Say)) or not at all (e.g., *Clivina impressifrons* (LeConte), and *Cyclotrachelus sodalis* (LeConte)) in this study. Some of these differences may be due to the habitats sampled. Two of the studies sampled both perennial and annual crop habitats, and *C. sodalis* (Clark et al. 1997) and *Pt. permundus* (Carmona and Landis 1999) were more common in the

Table 2. Total number of carabid beetles captured per species and percentage of total capture.

Species	Abundance per Habitat					Total Capture	% Total
	Corn	Forest	Road	Soy	Wheat		
Pterostichus melanarius (Illiger)	132	6	26	1	99	264	18.88
Amara aenea (DeGeer)	87	32	41	2	85	247	17.67
Agonum placidum (Say)	16	16	6	2	155	195	13.95
Poecilus lucublandus (Say)	58	16	3		33	110	7.87
Harpalus herbivagus (Say)	48	37	14		8	107	7.65
Chlaenius tricolor (Dejean)	22	19	3		55	99	7.08
Poecilus chalcites (Say)	27	5	4	2	41	79	5.65
Agonum cupripenne (Say)	4	1			43	48	3.43
Bembidion quadrimaculatum (Say)	26		5		3	34	2.43
Anisodactylus rusticus (Say)	6	21	4		1	32	2.29
Bembidion nitidum (Kirby)	4	1	1		23	29	2.07
Anisodactylus sanctaecrucis (Fabricus)	8	10		2	5	25	1.79
Elaphropus anceps (LeConte)	9	5	6		4	24	1.72
Harpalus affinis (Schrank)	3		1	1	18	23	1.65
Stenolophus comma (Fabricius)	4	5	4		1	14	1.00
Pterostichus pensylvanicus (LeConte)	2	10			1	13	0.93
Anisodactylus harrisii (LeConte)	2	5	1			8	0.57
Agonum muelleri (Herbst)	1	2			4	7	0.50
Diplocheila obtusa (LeConte)	1	4			1	6	0.43
Pterostichus permundus (Say)	1	1			2	4	0.29
Calosoma calidum (Fabricius)			1		2	3	0.21

Table 2. Continued.

| Species	Abundance per Habitat					Total Capture	% Total
	Corn	Forest	Road	Soy	Wheat		
Galerita bicolor (Drury)		2	1			3	0.21
Harpalus pensylvanicus (DeGeer)		1		1	1	3	0.21
Scarites quadriceps (Chaudoir)			2		1	3	0.21
Bembidion obtusum (Serville)	1	1				2	0.14
Bradycellus rupestris (Say)	1		1			2	0.14
Patrobus longicornis (Say)	1	1				2	0.14
Amphasia interstitialis (Say)		1				1	0.07
Bembidion rapidum (LeConte)		1				1	0.07
Bembidion versicolor (LeConte)	1					1	0.07
Calathus gregarious (Say)			1			1	0.07
Calleida punctata (LeConte)	1					1	0.07
Chlaenius impunctifrons (Say)					1	1	0.07
Chlaenius tomentosus (Say)	1					1	0.07
Harpalus puncticeps (Stephans)		1				1	0.07
Stenolophus ochropezus (Say)	1					1	0.07
Total	469	204	125	11	589	1398	100
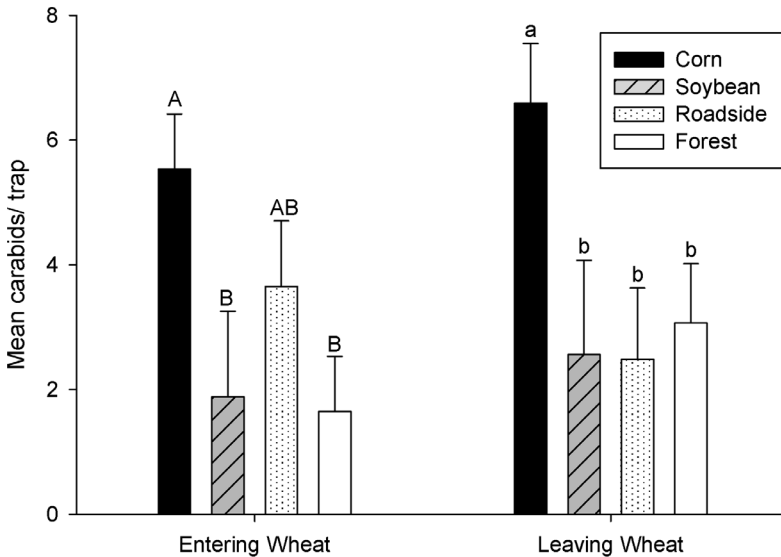
Figure 2. Mean (± SE) number of carabids per trap captured moving between wheat fields and adjacent habitats. Means sharing the same letter do not differ significantly (Tukey-Kramer post-hoc, $P > 0.05$).

perennial habitats. In other cases, differences in abundant species across studies may be related to interannual variation in carabid abundance. Even within a single habitat in a given study, the abundance of a particular carabid species may vary greatly from year to year (e.g., Lee et al. 2001, Rutledge et al. 2004).

Carabid community assemblages differed among field boundary types and wheat field centers. Both the identity and number of dominant species varied among habitats, including the presence and activity-density of species like *Ch. tricolor, Pt. melanarius* and *B. quadrimaculatum,* which are known to consume crop pests such as slugs (Bohan et al. 2000, Eskelson et al. 2011) and weevil eggs (Vankosky et al. 2011). This suggests that maintaining an agricultural ecosystem composed of a variety of both crop and non-crop habitats may help maintain these species in the landscape, supporting carabid diversity and abundance.

The community assemblage data should be interpreted cautiously due to the inherent limitations with the use of pitfall traps in different habitats. Pitfall traps measure activity-density, i.e., captures are influenced by both population sizes and activity levels. Dense vegetation at ground level restricts the freedom of carabid movement, such that carabid activity decreases as vegetation density increases (Frampton et al. 1995, Mauremooto et al. 1995, Thomas et al. 2006). Therefore, pitfall trap captures should not be used to compare population sizes in habitats with different vegetation density, as this cannot be separated from vegetation effects on activity. Here, we are less concerned with overall population sizes than with activity at the border between habitats. This study demonstrated that carabid movement is greater across certain boundary types than others. Variation in carabid preference for and community assemblage among the studied habitats may be due to microclimate differences. Factors such as soil surface temperature, humidity and ground cover can significantly influence carabid abundance and diversity by creating a more favorable or unfavorable microclimate (Chiverton and Sotherton 1991, Henshall et al. 2011, Ward et al. 2011). Carabids tend to

Table 3. The percent of captures at field boundaries for the most common carabid species. Only species contributing at least 5% at a given boundary are shown.

	Entering wheat fields				Leaving wheat fields			
	Corn	Soybean	Roadside	Forest	Corn	Soybean	Roadside	Forest
Am. aenea	27.37	5.71	24.81	23.60	22.83	7.69	35.69	9.96
B. quadrimaculatum	19.52	18.10	30.18	7.91	11.50	15.38	15.82	8.83
Pt. melanarius	16.93	15.24	9.21	10.10	19.03	24.16	7.07	14.48
Po. lucublandus	6.39				8.23			6.06
E. anceps	5.44					8.79		
Ag. placidum		20.00		8.05	5.04	17.58		5.54
Ch. tricolor		7.62		5.73		7.69		10.37
H. pensylvanicus		6.67						
H. herbivagus			5.63	6.82				6.88
An. sanctaecrucis				6.28				9.65
An. rusticus							8.08	

Table 4. Analysis of Similarity results for each habitat comparison. The α for each habitat comparison was adjusted via the Benjamini and Hochberg FDR Procedure with an original α of 0.05. Significance is indicated with an asterisk (*) when the P-value was less than or equal to the adjusted α –value.

Pair-wise comparisons	R-statistic	Permutations	P-value	Adjusted-α
Corn, forest	0.147	999	0.001*	0.005
Corn, soybean	0.472	999	0.001*	0.010
Corn, wheat	0.207	999	0.001*	0.015
Forest, wheat	0.271	999	0.001*	0.020
Road, wheat	0.415	999	0.001*	0.025
Soy, wheat	0.448	999	0.003*	0.030
Road, soy	0.566	495	0.008*	0.035
Forest, soy	0.269	999	0.022*	0.040
Corn, road	0.143	999	0.064	0.045
Forest, road	0.048	999	0.653	0.050

aggregate in refuges filled with dense vegetation in preference to bare ground (Brose 2003), although individual species may prefer microhabitats with more or less dense canopy cover (Ward et al. 2011). Dense vegetation and closed plant canopy can moderate microclimates by retaining soil moisture and decreasing soil surface temperature, as compared to bare soil exposed to sunlight.

By far, more carabids moved between wheat and corn than any other habitat studied. The most common species moving back and forth between corn and wheat are *Am. aenea*, *B. quadrimaculatum*, and *Pt. melanarius*. All three species are polyphagous predators of invertebrates (Sunderland 2002), and *Am. aenea* also consumes weed seeds (Tooley and Brust 2002). *Pt. melanarius* and *B. quadrimaculatum* are among the most common carabids found in North American agricultural fields (Luff 2002). *Pt. melanarius* and *Am. aenea* are eurytopic (Eversham et al. 1996), and are considered generalists of open habitats. For example, *Pt. melanarius* is able to forage in both crop and adjacent noncrop habitats of a variety of vegetation complexity and disturbance levels (Fournier and Loureau 2001). *Bembidion* species are known to be most active in crop habitats with bare ground and little shade (Luff 2002), such as cornfields (Esau and Peters 1975). Unsurprisingly, given their fairly generalized habitat use, these species were also active at the other boundary types.

The greater exchange rates between corn and wheat suggest that conditions in corn fields were more favorable for carabids than other habitats adjacent to wheat. Typically corn is planted before soybean in the North Central U.S., and thus corn on average closes canopy earlier in the summer growing season, creating a more favorable habitat for carabids for a greater portion of the summer. Conversely, the forest habitats monitored contained little understory
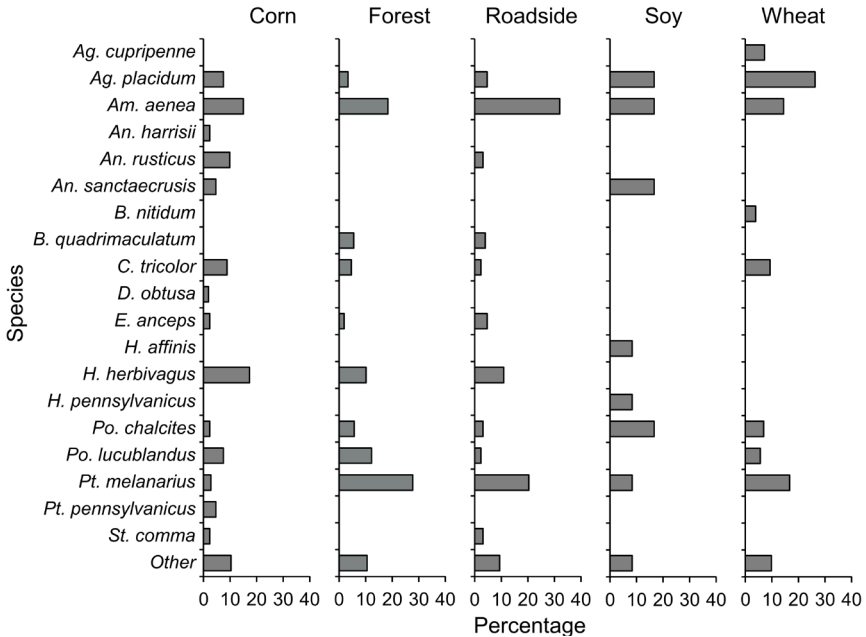

Figure 3. Percentages of each species composing total capture in corn, forest, roadside vegetation, soybean and wheat. Only the top species composing 90% of the total capture are listed individually and the remaining 10% are grouped together as "other".

vegetation, providing limited cover for carabids. Beetles are predicted to move more readily from high to low density vegetation than vice versa because of the way that dense vegetation slows carabid movement, retaining individuals closer to boundaries (Thomas et al. 2006). However, if that were the only mechanism at play, we would have expected to see high numbers of carabids leaving wheat for corn, which is a relatively open habitat a ground level due to plant spacing, but not high numbers moving from corn into wheat. The greater movement between these crops in both directions suggests that the effects of vegetation density on carabid movement were not the only factors at play.

Roadside vegetation also contributed moderate numbers of carabids to wheat fields. In our study, roadside vegetation consisted of densely growing grasses and weedy forbs, making this vegetation structure very different from an evenly planted crop field. Roadside vegetation could have provided alternative prey items and habitat structures that carabids find beneficial. Many studies have shown refuges such as these are crucial to carabid beetle populations because they provide overwintering sites (Desender 1982, Sotherton 1985, Desender and Alderweireldt 1988), alternative prey items (Hawthorne and Hassall 1995) and additional shelter during the spring and summer (Thomas et al. 2001), thereby enhancing populations and lowering the detrimental effects of disturbances such as harvest or pesticide application (Lee et al. 2001, Ward et al. 2011).

When considering the differences in carabid movement across boundaries, it is important to keep in mind that this study took place over a short time period during which little change in vegetation quality in any of the habitats occurred. Several studies have shown that both carabid abundance and diversity within crop fields and non-crop habitats vary over time as canopy traits change depending on the growth stage of the surrounding vegetation (Varchola and Dunn 1999, 2001). For example, it is likely that we would have seen more movement to and from grassy habitats had we sampled earlier in the season when carabids were emerging from their overwintering shelters or post-harvest. On-going studies will examine how the movement of carabids between various habitats changes throughout the growing season.

Studies examining the ability of agricultural landscapes to supply beneficial organisms to crop fields typically focus on the benefits of non-crop habitat (Burel et al. 2013). However, different crops can also provide different types of resources in the same way that non-crop habitats do (Fahrig et al. 2011). In fact, some populations may be able to persist by moving between ephemeral crop habitats that provide complementary resources without depending on more permanent habitats (Vasseur et al. 2013). Indeed, our results show more movement in and out of wheat from corn than from non-crop habitats during the portion of the season examined. Additionally, farmers may be more willing and able to manage the diversity and arrangement of crop habitats on their land than of non-crop habitats (Fahrig et al. 2011). Therefore, studies providing more detailed information about the potential benefits of crop habitats to natural enemies are critical for developing recommendations for designing agricultural landscapes to enhance biological control services.

Acknowledgments

Literature Cited

Asteraki, E. J., C. B. Hanks, and R. O. Clements. **1995**. The influence of different types of grassland field margin on carabid beetle (Coleoptera, Carabidae) communities. Agriculture Ecosystems and Environment 54: 195–202.

Blubaugh, C. K., V. A. Caceres, I. Kaplan, J. Larson, C. S. Sadof, and D. S. Richmond. **2011**. Ground beetle (Coleoptera: Carabidae) phenology, diversity, and response to weed cover in a turfgrass ecosystem. Environmental Entomology 40: 1093–1101.

Bohan, D. A., A. C. Bohan, D. M. Glen, W. O. C. Symondson, C. W. Wiltshire, and L. Hughes. **2000**. Spatial dynamics of predation by carabid beetles on slugs. Journal of Animal Ecology 69: 367–379.

Bohan, D. A., A. Boursault, D. R. Brooks, and S. Petit. **2011**. National-scale regulation of the weed seedbank by carabid predators. Journal of Applied Ecology 48: 888–898.

Bommarco, R. 1998. Reproduction and energy reserves of a predatory carabid beetle relative to agroecosystem complexity. Ecological Applications 8: 846–853.

Brose, U. 2003. Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135: 407–13.

Burel, F. 1989. Landscape structure effects on carabid beetles spatial patterns in western France. Landscape Ecology 2: 215–226.

Burel, F., C. Lavigne, E. J. P. Marshall, A. C. Moonen, A. Ouin, and S. L. Poggio. **2013**. Landscape ecology and biodiversity in agricultural landscapes. Agriculture, Ecosystems, and Environment 166: 1–2.

Carmona, D. M., and D. A. Landis. **1999**. Influence of refuge habitats and cover crops on seasonal activity- density of ground beetles (Coleoptera : Carabidae) in field crops. Environmental Entomology 1145–1153.

Chiverton, P. A., and N. W. Sotherton. **1991**. The effects on beneficial arthropods of the exclusion of herbicides from cereal crop edges. Journal of Applied Ecology 28: 1027–1039.

Clark, M. S., S. H. Gage, and J. R. Spence. **1997**. Habitats and management associated with common ground beetles (Coleoptera: Carabidae) in a Michigan agricultural landscape. Environmental Entomology 26: 519–527.

Clarke, K. R., and R. M. Warwick. **2001**. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed. PRIMER-E, Plymouth.

Desender, K. 1982. Ecological and faunal studies on Coleoptera in agricultural land. II. Hibernation of Carabidae in agro-ecosystems. Pedobiologia 23: 295–303.

Desender, K., and M. Alderweireldt. **1988**. Population dynamics of adult and larval carabid beetles in a maize field and its boundary. Journal of Applied Entomology 106: 13–19.

Esau, K. L., and D. C. Peters. 1975. Carabidae collected in pitfall traps in Iowa cornfields, fencerows, and prairies. Environmental Entomology 4: 509-513.

Eskelson, M. J., E. G. Chapman, D. D. Archbold, J. J. Obrycki, and J. D. Harwood. **2011**. Molecular identification of predation by carabid beetles on exotic and native slugs in a strawberry agroecosystem. Biological Control 56: 245–253.

Eversham, B. C., D. B. Roy, and M. G. Telfer. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. Annales Zoologici Fennici 33: 149-156.

Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J.-L. Martin. **2011**. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14: 101–112.

Fournier, E., and M. Loreau. 2001. Activity and satiation state in *Pterostichus melanarius:* an experiment in different agricultural habitats. Ecological Entomology 26: 235-244.

Frampton, G. K., T. Çilgi, G. L. A. Fry, and S. D. Wratten. **1995**. Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. Biological Conservation 71: 347–355.

French, B. W., L. D. Chandler, M. M. Ellsbury, B. W. Fuller, and M. West. **2004**. Ground beetle (Coleoptera: Carabidae) assemblages in a transgenic corn-soybean cropping system. Environmental Entomology 33: 554–563.

Gallandt, E. R., T. Molloy, R. P. Lynch, and F. A. Drummond. **2005**. Effect of cover-cropping systems on invertebrate seed predation. Weed Science 53: 69–76.

Gavish-Regev, E., Y. Lubin, and M. Coll. **2008**. Migration patterns and functional groups of spiders in a desert agroecosystem. Ecological Entomology 33: 202–212.

Hajek, A. E., J. J. Hannam, C. Nielsen, A. J. Bell, and J. K. Liebherr. **2007**. Distribution and abundance of Carabidae (Coleoptera) associated with soybean aphid (Hemiptera: Aphididae) populations in central New York. Annals of the Entomological Society of America 100: 876–886.

Hatteland, B. A., W. O. C. Symondson, R. A. King, M. Skage, C. Schander, and T. Solhøy. **2011**. Molecular analysis of predation by carabid beetles (Carabidae) on the invasive Iberian slug *Arion lusitanicus*. Bulletin of Entomological Research 101: 675–686.

Hawthorne, A., and M. Hassall. **1995**. The effect of cereal headland treatments on carabid communities, pp. 185–198. *In* Toft, S., Riedel, W. (eds.), Arthropod Natural Enemies in Arable Land I. Aarhus University Press, Aarhus.

Henshall, S. E., J. P. Sadler, D. M. Hannah, and A. J. Bates. **2011**. The role of microhabitat and food availability in determining riparian invertebrate distributions on gravel bars: a habitat manipulation experiment. Ecohydrology 4: 512–519.

Holland, J. M., M. Begbie, T. Birkett, S. Southway, and S. R. Thomas. **2004**. The spatial dynamics and movement of *Pterostichus melanarius* and *P . madidus* (Carabidae) between and within arable fields in the UK. International Journal of Ecology and Environmental Sciences 30: 35–53.

Holland, J. M., C. F. G. Thomas, T. Birkett, S. Southway, and H. Oaten. **2005**. Farm-scale spatiotemporal dynamics of predatory beetles in arable crops. Journal of Applied Ecology 42: 1140–1152.

Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. Agriculture Ecosystems and Environment 74: 187–228.

Landis, D. A., F. D. Menalled, A. C. Costamagna, and T. K. Wilkinson. **2005**. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. Weed Science 53: 902–908.

Lang, A. 2003. Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. Oecologia. 134: 144–153.

Lee, J. C., and D. L. Edwards. **2012**. Impact of predatory carabids on below- and above-ground pests and yield in strawberry. BioControl 57: 515–522.

Lee, J. C., F. B. Menalled, and D. A. Landis. **2001**. Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. Journal of Applied Ecology 38: 472–483.

Lindroth, C. H. 1961. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Opuscula Entomologica Supplementa XX, XXIV, XXIX, XXXIII, XXXIV, and XXXV. Berlingska Boktryckeriet, Sweden.

Lovei, G. L., and F. Szentkiralyi. **1984**. Carabids climbing maize plants. Zeitschrift Fur Angewandte Entomologie-Journal of Applied Entomology 97: 107–110.

Luff, M. L. 2002. Carabid assemblage organization and species composition, pp. 41-79. *In* Holland, J. M. (ed.), The Agroecology of the Carabid Beetles. Intercept Ltd, Andover, UK.

Mauremooto, J. R., S. D. Wratten, S. P. Worner, and G. L. A. Fry. **1995**. Permeability of hedgerows to predatory carabid beetles. Agriculture Ecosystems and Environment 52: 141–148.

Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. Annals of the Entomological Society of America 97: 240-248.

SAS Institute, Inc. 2009. SAS/STAT 9.2 User's Guide, Second Edition. SAS Institute, Inc., Cary, NC.

Sasakawa, K. 2010. Field observations of climbing behavior and seed predation by adult ground beetles (Coleoptera: Carabidae) in a lowland area of the temperate zone. Environmental Entomology 39: 1554–1560.

Schweiger, O., J. P. Maelfait, W. Van Wingerden, F. Hendrickx, R. Billeter, M. Speelmans, I. Augenstein, B. Aukema, S. Aviron, D. Bailey, R. Bukacek, F. Burel, T. Diekotter, J. Dirksen, M. Frenzel, F. Herzog, J. Liira, M. Roubalova, and R. Bugter. **2005**. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. Journal of Applied Ecology 42: 1129–1139.

Shearin, A. F., S. C. Reberg-Horton, and E. R. Gallandt. **2008**. Cover crop effects on the activity-density of the weed seed predator *Harpalus rufipes* (Coleoptera: Carabidae). Weed Science 56: 442–450.

Sotherton, N. W. 1985. The distribution and abundance of predatory Coleoptera over-wintering in field boundaries. Annals of Applied Biology 106: 17–21.

Sunderland, K.D. 2002. Invertebrate pest control by carabids, pp. 165-214. *In* Holland, J. M. (ed.), The Agroecology of the Carabid Beetles. Intercept Ltd, Andover, UK.

Sunderland, K. D., N. E. Crook, D. L. Stacey, and B. J. Fuller. **1987**. A study of feeding by polyphagous predators on cereal aphids using Elisa and gut dissection. Journal of Applied Ecology 24: 907–933.

Taboada, A., R. Tarrega, L. Calvo, E. Marcos, J. A. Marcos, and J. M. Salgado. **2010**. Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity. European Journal of Forest Research 129: 31–45.

Thomas, C. F. G., N. J. Brown, and D. A. Kendall. **2006**. Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. Agriculture, Ecosystems and Environment 113: 51–61.

Thomas, C. F. G., L. Parkinson, G. J. K. Griffiths, A. Fernandez Garcia, and E. J. P. Marshall. **2001**. Aggregation and temporal stability of carabid beetle distributions in field and hedgerow habitats. Journal of Applied Ecology 38: 100–116.

Tooley, J., and G. E. Brust. 2002. Weed seed predation by carabid beetles, pp. 215-229. *In* Holland, J. M. (ed.), The Agroecology of the Carabid Beetles. Intercept Ltd, Andover, UK.

Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. **2008**. Conservation biological control and enemy diversity on a landscape scale (Reprinted from Biol. Control, vol 43, pg 294-309, 2007). Biological Control 45: 238–253.

Vankosky, M. A., H. A. Cárcamo, and L. M. Dosdall. **2011**. Identification of potential natural enemies of the pea leaf weevil, *Sitona lineatus* L. in western Canada. Journal of Applied Entomology 135: 293–301.

Varchola, J. M., and J. P. Dunn. **1999**. Changes in ground beetle (Coleoptera: Carabidae) assemblages in farming systems bordered by complex or simple roadside vegetation. Agriculture Ecosystems and Environment 73: 41–49.

Varchola, J. M., and J. P. Dunn. **2001**. Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. Agriculture Ecosystems and Environment 83: 153–163.

Vasseur, C. 2012. Contrôles exercés par les mosaïques de systèmes de culture sur les dynamiques du carabe *Pterostichus melanarius* Illiger (Coleoptera: Carabidae). INRA SAD Paysage. Thèse de Doctorat, Universitéde Rennes 1.

Vasseur, C., A. Joannon, S. Aviron, F. Burel, J. M. Meynard, and J. Baudry. **2013**. The cropping systems mosaic: how does the hidden heterogeneity of agricultural landscapes drive arthropod populations? Agriculture, Ecosystems and Environment 166: 3–14.

Verhoeven, K. J. F., K. L. Simonsen, and L. McIntyre. **2005**. Implementing false discovery rate control: increasing your power. Oikos 108: 643–647.

Wallin, H., and B. S. Ekbom. **1988**. Movements of carabid beetles (Coleoptera, Carabidae) inhabiting cereal fields: a field tracing study. Oecologia 77: 39–43.

Ward, M. J., M. R. Ryan, W. S. Curran, M. E. Barbercheck, and D. A. Mortensen. **2011**. Cover crops and disturbance influence activity density of weed seed predators *Amara aenea* and *Harpalus pensylvanicus* (Coleoptera: Carabidae). Weed Science 59: 76–81.

Weibull, A. C., O. Ostman, and A. Granqvist. **2003**. Species richness in agroecosystems: the effect of landscape, habitat and farm management. Biodiversity and Conservation 12: 1335–1355.

Werling, B. P., and C. Gratton. **2008**. Influence of field margins and landscape context on ground beetle diversity in Wisconsin (USA) potato fields. Agriculture Ecosystems and Environment 128: 104–108.

White, S. S., K. A. Renner, F. D. Menalled, and D. A. Landis. **2007**. Feeding preferences of weed seed predators and effect on weed emergence. Weed Science 55: 606–612.

Winder, L., C. J. Alexander, J. M. Holland, W. O. C. Symondson, J. N. Perry, C. Woolley, C. J. Alexandert, J. M. Hollandi, and J. O. E. N. Perryt. **2005**. Predatory activity and spatial pattern : the response of generalist carabids to their aphid prey. Journal of Animal Ecology 74: 443–454.

Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: A template for biological control in annual crop systems. Biological Control 10: 4–15.