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Impacts of Contrasting Alfalfa Production Systems on the Drivers of Carabid Beetle (Coleoptera: Carabidae) Community Dynamics

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ABSTRACT Growing concerns about the environmental consequences of chemically based pest control strategies have precipitated a call for the development of integrated, ecologically based pest management programs. Carabid or ground beetles (Coleoptera:Carabidae) are an important group of natural enemies of common agricultural pests such as aphids, slugs, and other beetles. Alfalfa (*Medicago sativa* L.) is one of the most common forage crop species in the semi-arid western United States. In 2011, Montana alone produced 4.0×10^6 Mg of alfalfa on 8.1×10^5 ha for gross revenue in excess of US\$$4.3 \times 10^8$, making it the third largest crop by revenue. We conducted our study over the 2012 and 2013 growing seasons. Each year, our study consisted of three sites each with adjacent systems of monoculture alfalfa, alfalfa nurse cropped with hay barley, and an uncultivated refuge consisting of a variety of forbs and grasses. Carabid community structure differed and strong temporal shifts were detected during both 2012 and 2013. Multivariate fuzzy set ordination suggests that variation in canopy height among the three vegetation systems was primarily responsible for the differences observed in carabid community structure. Land managers may be able to enhance carabid species richness and total abundance by creating a heterogeneous vegetation structure, and nurse cropping in particular may be effective strategy to achieve this goal.

KEY WORDS Carabidae, community assembly, conservation biocontrol, alfalfa production, multivariate fuzzy set ordination

Growing concerns about the environmental consequences of chemically based pest control strategies have precipitated a call for the development of integrated, ecologically based pest management programs (Altieri et al. 1983, Matson et al. 1997, Robertson and Swinton 2005). Instead of relying primarily on synthetic inputs, these programs are based on augmenting ecological processes to stabilize or manage pest populations (Liebman and Gallandt 1997, Magdoff 2007, Altieri et al. 2012). Conservation biological control, in which a producer manipulates the ecological conditions in their system to enhance populations of natural enemies, is one such strategy (Barbosa 1998). Habitat management is a subset of conservation biocontrol that includes altering disturbance spatio-temporal regimes to decrease natural enemy mortality, improving shelter or microclimatic conditions to prevent their emigration, or providing refugia to which they can escape during management-imposed disturbances (Landis et al. 2000).

Carabid or ground beetles (Coleoptera:Carabidae) are an important group of natural enemies of common agricultural pests such as aphids, slugs, and other beetles (Holland 2002, Sunderland 2002). They comprise one of the most abundant and diverse families of beetles and are abundant and ubiquitous in northern temperate agroecosystems (Lovei and Sunderland 1996). Many carabid beetle species, especially those in the Zabrini and Harpalini tribes, are seed predators and may help regulate weed populations (Tooley and Brust 2002, Menalled et al. 2007, Gaines and Gratton 2010). For these reasons, carabids are often regarded as target species of conservation biocontrol. However, many carabid species have very specific habitat preferences and are highly sensitive to changes in their environment (Lovei and Sunderland 1996). Thus, habitat management practices could have important ramifications for carabid beetle conservation in highly disturbed agricultural systems.

Alfalfa (*Medicago sativa* L.) is one of the most common forage crop species in the semi-arid western United States (Putnam et al. 2000). In 2011, Montana alone produced 4.0×10^6 Mg of alfalfa on 8.1×10^5 ha for gross revenue in excess of US\$$4.3 \times 10^8$, making it the third largest crop by revenue and area harvested in the state after spring and winter wheat (*Triticum aesativum* L.; National Agricultural Statistics Service [NASS] 2013). A major threat to alfalfa production is herbivory by insect pests such as the alfalfa weevil (*Hypera postica* Gyllenhal), aphids (Hemiptera: Aphididae), and cutworms (Lepidoptera: Noctuidae) (Summers 1998, Brewer and Hoff 2002, Salisbury 2004). For example, herbivory by the alfalfa weevil alone can result in yield losses of up to 30–40% in the Intermountain West of the United States (Salisbury 2004).

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In contrast to most other major commodities in the region, alfalfa is a perennial crop, thus providing temporally stable habitat for insect pests as well as their natural enemies, including carabids (Summers 1998). Therefore, habitat management to enhance natural carabid communities in alfalfa could be an important ecologically based component of an integrated pest management strategy (Clark et al. 1997). Specifically, increasing plant diversity at both the within-field (α-diversity) and between-field (β-diversity) scales may help assemble a more diverse array of natural enemies and thereby enhance biological control (Altieri and Letourneau 1982, Altieri 1999, Benton et al. 2003, Letourneau et al. 2011).

Barbosa and Wratten (1998) argue that habitat management is only an effective means of conservation biological control if the natural enemy populations have the proper spatial and temporal distribution within an agroecosystem. Thus, understanding the community dynamics of target natural enemies and how those dynamics relate to changes in the environment is imperative for proper habitat management. Nurse cropping (also known as relay cropping or companion cropping), in which one species with a short life cycle is grown simultaneously with a second, longer-lived species, is a method by which to increase vegetative α-diversity in agroecosystems (Roslon and Fogelfors 2003). Nurse cropping can provide a variety of agronomic benefits including weed suppression, soil stabilization, alternative sources of revenue, and pest management (Canevari 2000). Uncultivated areas within farmlands can increase β-diversity as they may provide refugia or alternative habitats to natural enemies (Lee et al. 2001, Lee and Landis 2002, Gaines and Gratton 2010).

While many studies conducted in agroecosystems have compared carabid community structure among habitat types (Kromp 1989, Östman et al. 2001, MacLeod et al. 2004, Lövei et al. 2006, Menalled et al. 2007, Gaines and Gratton 2010), few have directly investigated the temporal dynamics or the influence of vegetative architecture on carabid communities (but see Gardner et al. 1997). Increased understanding of the drivers of carabid community dynamics can help inform better habitat management practices in alfalfa production for carabid conservation. In this study, we assessed carabid beetle community dynamics and its relationship with vegetative architecture in three alfalfa production systems: monoculture alfalfa, alfalfa nurse cropped with barley (*Hordeum vulgare* L.), and uncultivated areas. Our first objective was to relate carabid activity-density with vegetative architecture as well as time within the growing season to understand the drivers of carabid community dynamics. Our second objective was to develop a predictive model of the most abundant species of carabids as a function of vegetative architecture.

Materials and Methods

Site Description. This research was conducted on the Sieben Ranch in Helena, MT (WGS 84 46° 41.40′ N, 112° 0.02′ W). The site is underlain with Thess-Series loam (fine loamy over sandy or sandy skeletal, superactive, frigid, Aridic, Calciusteps), receives ∼250–355 mm of precipitation annually, and has a mean annual air temperature of 2.8–7.2°C (Natural Resources Conservation Service [NRCS] 2013).

Study Design. We conducted our study over the 2012 and 2013 growing seasons. Each year, our study consisted of three sites each with adjacent systems of monoculture alfalfa, alfalfa nurse cropped with hay barley ("barley nurse crop" hereafter) and an uncultivated refuge consisting of a variety of forbs and grasses (Table 1). At each site, we set up three subsample plots within each system to assess carabid beetle community structure using pitfall traps. A subsample plot consisted of three pitfall traps arranged in an equilateral triangle with 10 m sides. The subsample plots were at least 100 m from any field boundary and were spaced 100 m apart. To construct the pitfall traps, we dug ∼20–30-cm-deep × 10-cm-wide holes with a post-hole auger and placed two stacked 0.5-liter plastic cups (Solo Cup Company, Lake Forest, IL) in each of those holes. We backfilled the pitfall trap holes until the mouth of the top cup was flush with the soil surface and filled the top cup of the pitfall trap approximately one-third full with propylene glycol-based antifreeze (Arctic Ban, Camco Manufacturing Inc., Greensboro, NC). Each pitfall trap was covered with a rain cover constructed from a 25-cm-diameter clear plastic plate held to the ground with three equally spaced 10-cm bolts. All rain covers had at least 2 cm between the soil surface and the rim of the clear plastic plates to avoid interfering with ground dwelling arthropod activity.

To accommodate farming activities, pitfall traps installation and removal dates varied among systems and between years (Fig. 1). Early in the growing season, we installed the pitfall traps at each subsample in the uncultivated refuge and monoculture alfalfa systems. Once the barley nurse crop was seeded, we installed pitfall traps into the barley nurse crop fields. Pitfall traps from all monoculture alfalfa fields were removed to allow the producer to harvest. Pitfall traps were reinstalled in the monoculture alfalfa fields following harvest. In 2012, we removed the pitfall traps from all barley nurse crop fields to allow the producer to harvest and did not reinstall them for the remainder of the growing season. Uncultivated refuge pitfall traps were removed both years to allow the producer to stack baled hay. In 2012, these pitfall traps were not reinstalled for the remainder of the growing season, but in 2013 were reinstalled after the producer finished baling activities.

While installed, each week we collected all arthropods caught in the pitfall traps by placing them in an 11.5 × 23 cm plastic bag (Whirl-Pak, Nasco Inc., Fort Atkinson, WI). Following collection, all pitfall traps were replenished with antifreeze for sampling the subsequent week. We sorted all subsamples for carabid beetles, transferred them to 70% by volume ethanol and identified them to species in the laboratory following Lindroth (1969). All species names follow Bousquet (2012). Carabid voucher specimens are maintained in Marsh Lab Rm 59, Department of Animal and Range

Table 1. Vegetation cover and plant community structure in uncultivated refuge systems in 2012 and 2013 at Sieban Ranch, Helena, MT

		2012			2013		
		Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
Stand Cover	Live Vegetation	35%	45%	35%	45%	40%	50%
	Thatch	5%	10%	15%	50%	20%	20%
	Bare ground	60%	45%	50%	10%	40%	30%
Species Cover	*Medicago sativa* (L.)	19%		39%	15%	45%	21%
	Descurania sophia (L.) Webb ex Prantl	36%	3%	40%	1%	5%	5%
	Descurania pinnata (Walter) Britton	14%					1%
	Bromus inermis (Leyss.)	31%	85%	21%	67%	31%	66%
	Dactylis glomerata (L.)		7%	1%	2%	4%	6%
	Poa pratensis (L.)		1%		15%	1%	
	Melilotus officianalis (L.)		5%				
	Cirsium vulgare (L.)					1%	
	Taraxicum officinale (L.)						1%
	Cardaria draba (L.) Desv.					4%	
	Cirsium arvensis (L.)					10%	

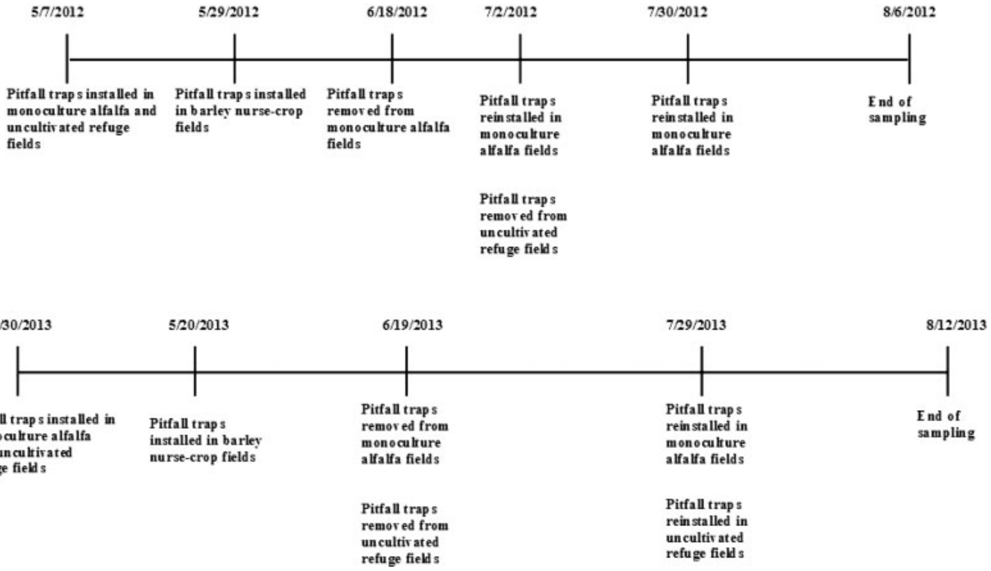

Fig. 1. Pitfall trap installation and removal dates for carabid beetle sampling in 2012 and 2013 at Sieban Ranch, Helena, MT.

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One limitation of pitfall trapping is that the probability of capturing a beetle depends on both how many beetles are in a given area and how much those beetles are moving (Luff 2002). Thus, pitfall trapping confounds activity and density. Entomologists, therefore, refer to values obtained from pitfall trapping as “activity-density,” and treat those values as metrics of relative abundance (Kromp 1989). Additionally, because in our study beetles were free to disperse between fields, our results reflect habitat selection rather than changes in carabid populations *per se* (Lee et al. 2001). While these limitations have been well documented in the literature, pitfall trapping remains one of the most efficient methods for sampling carabid beetles (Greenslade 1964, Kromp 1989, Spence and Niemelä 1994, Lee et al. 2001, Luff 2002).

Each time pitfall traps were collected, we measured the vegetation canopy height and percent cover for each subsample. Canopy height was estimated by randomly placing a meter stick at five locations in each subsample and recording the height of the tallest plant. The five measurements were averaged prior to data analysis. Percent cover was measured by randomly tossing a 0.5-m^2 wire hoop in each subsample and visually estimating the percent bare ground within the hoop.

Our study was conducted as on-farm research and sampling intensity and timing varied among vegetation types to allow for farm operations. While a lack of investigator control has been noted as a drawback to on-farm research (Molnar et al. 1992), such research programs often provide more realistic results (Tanaka et al. 2008, Meynard et al. 2012). Thus, while we suggest that readers exercise caution when interpreting our results, we believe they are an informative and realistic assessment of carabid community dynamics as a function of habitat management.

Data Analysis. We analyzed the effects of vegetation canopy height and percent bare ground on carabid beetle community structure using multivariate fuzzy set ordination (MFSO) on a Bray–Curtis dissimilarity matrix (Roberts 1986). Prior to constructing the dissimilarity matrix, the raw data were log-transformed to de-emphasize the effect of dominant species according to:

$$T_{ij} = ln\left(a_{ij} + 1\right) \tag{1}$$

where T_{ij} is the log-transformed activity-density of species i in community j and a_{ij} is the raw abundance of species i in community j. Bray–Curtis dissimilarity was calculated as:

$$BC_{jk} = \frac{\sum_{i=1}^{S} 2|T_{ij} - T_{ik}|}{\sum_{i=1}^{S} T_{ij} + \sum_{i=1}^{S} T_{ik}} \tag{2}$$

where BC_{ij} is the dissimilarity between sites j and k, T_{ij} and T_{ik} are the log-transformed activity-density of species i in sites j and k, respectively, and S is the combined total number of species in both communities (Bray and Curtis 1957, McCune et al. 2002). Two major advantages MFSO over other constrained ordination methods such as canonical correspondence analysis and redundancy analysis are that MFSO ordination axes correspond directly to environmental gradients and that MFSO detrends autocorrelated predictors to avoid confounding effects of non-independent environmental gradients (Roberts 2009).

We compared carabid community structure among vegetation types using a permutation multivariate analysis of variance (PERMANOVA) on a log-transformed Bray–Curtis dissimilarity matrix of species activity-densities with 9999 Monte Carlo iterations (Anderson 2005). Because we sampled the same plots on multiple dates, we used the Julian date of collection as a covariate in the PERMANOVA. Canopy height and canopy cover are autocorrelated with Julian date, and these covariates were not included in the analysis. For each year, PERMANOVA tests for overall differences in carabid community structure by vegetation type and for temporal shifts in carabid community structure were conducted separately. In addition, these analyses were conducted separately for each year of our study.

To assess the overall effects of habitat management on carabid communities, we compared mean weekly carabid activity-density, total species richness, and α-diversity among vegetation types from data pooled across all sampling dates. A Box–Cox power transformation analysis indicated that a log-transformation was warranted for activity-density. These metrics were compared using ANOVA with vegetation type blocked by site and $\alpha = 0.05$. We quantified α-diversity using Simpson's Diversity Index (1 – D):

$$D = \sum_{i=1}^{S} p_i^2 \tag{3}$$

where p_i is proportion that species i comprises in a community and S is the total number of species in that community (Simpson 1949).

We compared canopy height and percent bare ground among monoculture alfalfa, barley nurse crop, and uncultivated refuge fields using ANCOVA with Julian date as a covariate. An omnibus ANCOVA was conducted separately for each year to test for main effects. Pairwise ANCOVA models were constructed to compare slope differences between vegetation types. Because of concerns of spurious inference, we ignored intercept differences because planting dates varied among the three vegetation types.

Finally, to investigate habitat preferences among the most common carabids, we created a predictive model for the activity-density of the three species with the greatest total number of specimens collected within each vegetation system (*Pterostichus melanarius* Illiger, *Agonum placidum* Say, and *Agonum cupreum* Dejean). Candidate predictors of activity-density included canopy height, Julian date of the sampling period, and percent bare ground. Our models of activity-density were constructed using quasi-Poisson regression owing to concerns of overdispersion (Maindonald and Braun 2006). Model selection was performed by comparing reduction in residual deviance (ΔD) among candidate models beginning with a full model of all three predictors and dropping one predictor at a time. Data from both 2012 and 2013 were pooled prior to constructing the predictive models to allow for more generalizable models.

All statistics and graphics were performed in R version 3.0.2 (R Development Core Team 2013, Vienna, Austria). Community indices and PERMANOVA were calculated in the vegan (Oksanen et al. 2007) and labdsv (Roberts 2007) packages of R. Ordinations were calculated and graphed using the cluster (Maechler et al. 2012), fso (Roberts 2010), and rgl (Adler and Murdoch 2008) packages. All other graphics were created using the ggplot2 (Wickham 2009) and sciplot (Morales et al. 2010) packages. Post hoc tests for significant interactions found from ANOVA were conducted using Tukey's honestly significant difference in the TukeyC package (Jelihovschi and Allaman 2011).

Results

We captured a total of 15,106 carabid beetle specimens from 59 species in 2012 and 12,336 specimens from 47 species in 2013. Over 85% of all beetles caught in 2012 were members of just six species: *Pterostichus melanarius* (Illiger) ($n = 9{,}144$; 60.5% of all beetles captured), *Agonum placidum* (Say) ($n = 2{,}080$; 13.8%), *Agonum cupreum* (Dejean) ($n = 972$; 6.4%), *Bradycellus congener* (LeConte) ($n = 383$; 2.5%), *Agonum* *cupripenne* (Say) ($n = 316$; 2.1%), and *Harpalus amputatus* (Say) ($n = 298$; 2.0%). In 2013, over 90% of all specimens were members of just three species: *P. melanarius* ($n = 7{,}975$; 64.6%), *A. placidum* ($n = 2{,}625$, 21.3%), and *A. cupreum* ($n = 589$; 4.7%). The activity-densities of *P. melanarius* and *A. placidum*, our two most frequently captured species, were greatest in the barley nurse crop fields in both 2012 and 2013. The activity-density of our third most commonly collected species, *A. cupreum*, was greatest in monoculture alfalfa fields in 2012, but was greatest in barley nurse crop fields in 2013 (Table 2).

Based on species composition and activity-density, the PERMANOVA indicated that carabid community structure differed among vegetation systems sampled in 2012 (pseudo-$F = 4.25$; df = 2, 6; $r^2 = 0.59$; $P = 0.007$; Table 2). In addition, there were strong temporal shifts in the carabid communities of our three studied systems (pseudo-$F = 11.17$; df = 1, 74; $r^2 = 0.10$; $P < 0.001$). The MFSO revealed that variation in canopy height among the three vegetation systems in 2012 was primarily responsible for these differences observed in carabid community structure (Fig. 2A–C). Points that are closer in ordination space have community structures that more closely resemble each other, whereas those farther apart in ordination space have more dissimilar community structures. Axis values of MFSO are the fuzzy set membership of each sample to the corresponding environmental gradient. Membership values reflect the estimated value of the environmental gradient based on the dissimilarity of a given community to the communities on either extreme of the gradient (Roberts 1986). While canopy height had only a marginally significant impact on carabid community structure in 2012 ($r^2 = 0.63$; $P = 0.10$), it was the strongest ecological filter structuring carabid communities as that ordination axis had the greatest spread of communities. Communities with the same apparent canopy height had different apparent dates in the ordination, suggesting that date of the growing season modified the effect of canopy height on carabid community structure ($r^2 = 0.05$; $P = 0.01$). Finally, percent bare ground (estimated by ground cover) modified the impacts of canopy height and date within the growing season on carabid communities, with uncultivated refuge systems having higher apparent bare ground than either barley nurse crop or monoculture alfalfa systems at similar values of apparent canopy height and apparent date in the ordination ($r^2 = 0.03$; $P = 0.01$).

In 2013, carabid community structure also differed among the three vegetation types (pseudo-$F = 5.98$; df = 2,6; $r^2 = 0.67$; $P = 0.005$; Table 2). As in 2012, there were temporal shifts in carabid community structure within each vegetation type (pseudo-$F = 10.94$; df = 1,65; $r^2 = 0.11$; $P = 0.0001$). Similar to our observations in 2012, the MFSO showed that variation in canopy height among the three vegetation systems was the main driver of the observed differences in carabid communities (Fig. 2D–F). Despite having only a marginally significant effect, canopy height again was the strongest ecological filter affecting carabid communities as this ordination axis accounted for the greatest amount of variation in community structure ($r^2 = 0.50$; $P = 0.07$). Date of the growing season modified the impact of canopy height on carabid community structure, so that communities were dissimilar on different dates despite having the same apparent canopy height ($r^2 = 0.07$; $P = 0.02$). In contrast to the results observed in 2012, percent bare ground did not modify the effects of either canopy height or date of the growing season on carabid community structure, as there was little variation along this ordination axis ($r^2 = 0.007$; $P = 0.55$).

Carabid beetle activity-density differed among vegetation systems in both 2012 and 2013 (Table 3). In 2012, activity-density was greater in barley nurse crop systems than in refuge systems ($P = 0.02$; Fig. 3A), but it did not differ between barley nurse crop and monoculture alfalfa systems ($P = 0.56$). Activity-density was marginally greater in monoculture alfalfa systems than in uncultivated refuge areas ($P = 0.06$) in 2012. In 2013, carabid activity-density was greater in barley nurse crop systems than in either monoculture alfalfa systems ($P = 0.03$) or uncultivated refuge areas ($P = 0.008$), but it did not differ between monoculture alfalfa systems and uncultivated refuge areas ($P = 0.23$; Fig. 3D). Carabid species richness did not differ among vegetation systems in either 2012 (Table 3; Fig. 3B) or 2013 (Table 3; Fig. 3E). While α-diversity did not differ among the three vegetation systems in 2012 (Table 3; Fig. 3C), we found in 2013 that uncultivated refuge areas had higher diversity than in either barley nurse crop ($P < 0.001$; Table 3; Fig. 3F) or monoculture alfalfa systems ($P < 0.001$). Monoculture alfalfa systems, in turn, had higher α-diversity than did barley nurse crop systems ($P < 0.001$).

Changes in canopy height during the growing season differed among monoculture alfalfa, barley nurse crop, and uncultivated refuge systems in both 2012 ($F = 71.45$; adjusted $r^2 = 0.82$; df = 5, 72; $P < 0.001$; Fig. 4A) and 2013 ($F = 28.79$; adjusted $r^2 = 0.67$; df = 5, 63; $P < 0.001$; Fig. 4B). In 2012 and 2013, we found that the canopy increased height faster in barley nurse crop systems than in either monoculture alfalfa ($t = 8.49$; $P < 0.001$ and $t = 5.93$, $P < 0.001$, respectively) or in uncultivated refuge systems ($t = 7.23$, $P < 0.001$ and $t = 8.28$, $P < 0.001$, respectively). During both years of this study, there was no difference in the rate of change in canopy height between monoculture alfalfa or uncultivated refuge systems ($t = 0.19$, $P = 0.85$ and $t = -0.53$, $P = 0.60$ for 2012 and 2013, respectively).

Changes in percent bare ground varied among our three systems in 2012 ($F = 13.68$; df = 5, 72; $P < 0.001$; Fig. 5A) and in 2013 ($F = 33.66$; df = 5, 63; $P < 0.001$, Fig. 5B). In 2012, the canopy closed faster, as indexed by change in percent bare ground, in barley nurse crop systems than in either monoculture alfalfa ($t = 5.90$; $P < 0.001$) or uncultivated refuge systems ($t = -4.23$; $P < 0.001$). Likewise, canopy closure was faster in the barley nurse crop than in either of the other two systems in 2013 (monoculture alfalfa: $t = -8.00$; $P < 0.001$; uncultivated refuge: $t = -5.92$; $P < 0.001$). However, we did not detect a difference in the rate of

Table 2. Mean weekly carabid beetle captures from May 2012–August 2012 and from May 2013–August 2013 in monoculture alfalfa, barley nurse crop, and uncultivated refuge fields at Sieban Ranch, Helena, MT

Species	2012			2013		
	Alfalfa	Barley nurse crop	Refuge	Alfalfa	Barley nurse crop	Refuge
Agonum cupreum (Dejean)	63.1 ± 15.7	41.6 ± 11.9	1.0 ± 0.7	26.7 ± 5.8	50.1 ± 12.8	0.3 ± 0.3
Agonum cupripenne (Say)	22.4 ± 12.8	11.5 ± 5.3		4.9 ± 2.1	12.4 ± 8.7	
Agonum placidum (Say)	24.2 ± 7.1	229.6 ± 68.7	0.1 ± 0.1	9.4 ± 3.5	318.8 ± 113.7	1.1 ± 0.4
Amara apricaria (Paykull)		0.1 ± 0.1				
Amara cupreolata (Putzeys)	8.8 ± 3.2	2.5 ± 0.8	3.1 ± 1.1	14.6 ± 4.1	3.8 ± 0.9	7.5 ± 2.1
Amara familiaris (Duftschmid)						0.1 ± 0.1
Amara farcta (LeConte)	4.6 ± 2.0	2.8 ± 1.8	20.0 ± 6.3	1.3 ± 0.4	1.4 ± 0.7	2.3 ± 0.9
Amara idahoana (Casey)	0.1 ± 0.1					
Amara littoralis (Dejean)	14.8 ± 3.7	2.3 ± 1.0	12.1 ± 3.8	7.0 ± 1.7	2.3 ± 0.6	4.0 ± 2.2
Amara obesa (Say)	0.4 ± 0.2	0.9 ± 0.4	0.8 ± 0.4	0.6 ± 0.2	0.4 ± 0.4	13.9 ± 9.6
Amara quenseli (Schönherr)	0.7 ± 0.3	0.3 ± 0.2	0.9 ± 0.5			0.5 ± 0.4
Amara thoracica (Hayward)	0.8 ± 0.2	0.3 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	
Anisodactylus harrisi (LeConte)			0.1 ± 0.1			0.1 ± 0.1
Bembidion bimaculatum (Kirby)		0.1 ± 0.1				
Bembidion concolor (Kirby)					0.1 ± 0.1	
Bembidion nigripes (Kirby)				0.1 ± 0.1		
Bembidion nitidum (Kirby)	0.1 ± 0.1	20.9 ± 15.8	2.6 ± 1.0	0.1 ± 0.1	1.5 ± 1.5	0.3 ± 0.2
Bembidion obscurellum (Motschulsky)	0.1 ± 0.1	0.4 ± 0.3	0.1 ± 0.1			
Bembidion quadrimaculatum dubitans (LeConte)	3.3 ± 1.9	13.0 ± 8.9	1.5 ± 1.2	2.4 ± 1.4	3.1 ± 2.4	0.1 ± 0.1
Bembidion rapidum (LeConte)	1.9 ± 1.0	4.1 ± 1.3	0.1 ± 0.1		0.1 ± 0.1	
Bembidion rupicola (Kirby)	0.3 ± 0.2	0.5 ± 0.2	0.1 ± 0.1	0.4 ± 0.3		
Bembidion timidum (LeConte)		0.1 ± 0.1				
Bembidion versicolor (LeConte)	2.3 ± 1.2	3.0 ± 1.5	1.0 ± 1.0	2.4 ± 1.7	1.4 ± 0.8	0.0 ± 0.0
Bradycellus congener (LeConte)	35.1 ± 32.0	0.8 ± 0.5	3.3 ± 2.2	4.3 ± 3.1		0.4 ± 0.2
Bradycellus neglectus (LeConte)	0.1 ± 0.1					
Bradycellus nigerrimus (Lindroth)		0.3 ± 0.3				
Calosoma cancellatum (Eschscholtz)	0.1 ± 0.1	0.9 ± 0.6		0.1 ± 0.1	0.9 ± 0.5	
Calosoma lepidum (LeConte)	0.3 ± 0.2	0.5 ± 0.3			1.1 ± 0.5	0.1 ± 0.1
Calosoma obsoletum (Say)		0.5 ± 0.3			0.8 ± 0.6	
Carabus nemoralis (Müller)	0.1 ± 0.1		0.1 ± 0.1			0.5 ± 0.5
Chlaenius impunctifrons (Say)	0.2 ± 0.2	0.3 ± 0.3		0.1 ± 0.1		
Chlaenius purpuricollis (Randall)				0.1 ± 0.1		
Chlaenius sp. (Bonelli)					0.1 ± 0.1	0.0 ± 0.0
Chlaenius tomentosus (Say)		0.1 ± 0.1				
Cicindela purpurea audobonii (LeConte)		0.1 ± 0.1				
Clivina fossor (L.)	0.5 ± 0.3	0.4 ± 0.3				
Clivina impressifrons (LeConte)	0.2 ± 0.2					
Harpalus affinis (Schrank)		0.1 ± 0.1				
Harpalus amputatus (Say)	7.2 ± 1.1	16.6 ± 3.4	11.6 ± 2.6	3.9 ± 0.9	4.4 ± 1.1	2.6 ± 0.5
Harpalus desertus (LeConte)	0.2 ± 0.1	0.8 ± 0.3	6.0 ± 2.2		0.1 ± 0.1	0.1 ± 0.1
Harpalus erraticus (Say)	0.1 ± 0.1				0.0 ± 0.0	0.0 ± 0.0
Harpalus fraternus (LeConte)	0.5 ± 0.3	7.4 ± 2.4	0.5 ± 0.3	0.1 ± 0.1	1.1 ± 0.5	0.6 ± 0.3
Harpalus fuscipalpis (Sturm)	0.2 ± 0.1	3.8 ± 1.5	14.6 ± 4.2	0.3 ± 0.3	0.4 ± 0.3	3.0 ± 2.0
Harpalus nigritarsis (Sahlberg)	0.6 ± 0.3	0.9 ± 0.4	0.6 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	6.9 ± 3.0
Harpalus opacipennis (Haldeman)	0.1 ± 0.1	1.6 ± 0.9	1.4 ± 0.4		0.1 ± 0.1	0.8 ± 0.4
Harpalus pensylvanicus (DeGeer)	0.3 ± 0.3				0.3 ± 0.3	0.0 ± 0.0
Harpalus reversus (Casey)	0.3 ± 0.2	3.8 ± 1.3	3.1 ± 2.8	0.1 ± 0.1	1.1 ± 0.7	0.4 ± 0.2
Harpalus somnulentus (Dejean)	0.4 ± 0.2	0.5 ± 0.2	1.5 ± 0.5	0.4 ± 0.2	0.5 ± 0.4	1.6 ± 0.6
Harpalus sp. (Latreille)					0.1 ± 0.1	
Harpalus ventralis (LeConte)	0.4 ± 0.3	1.3 ± 0.4	0.1 ± 0.1		0.3 ± 0.2	0.9 ± 0.6
Lebia guttula (LeConte)	0.1 ± 0.1					
Lebia solea (Hentz)			0.1 ± 0.1	0.3 ± 0.3		0.8 ± 0.5
Loricera pilicornis (F.)	5.1 ± 1.0	0.8 ± 0.4	0.1 ± 0.1	2.1 ± 0.8	0.1 ± 0.1	
Microlestes linearis (LeConte)	6.0 ± 3.4	4.1 ± 2.0	6.9 ± 2.6	1.0 ± 1.0	1.3 ± 0.6	6.5 ± 2.8
Notiophilus simulator (Fall)	0.1 ± 0.1		0.1 ± 0.1			
Piosoma setosum (LeConte)		0.3 ± 0.2	0.1 ± 0.1			
Poecilus corvus (LeConte)	1.3 ± 0.7	0.3 ± 0.2		1.4 ± 0.7	2.4 ± 1.1	
Poecilus lucublandus (Say)	2.8 ± 1.0	1.0 ± 0.7		1.9 ± 1.1	2.6 ± 0.8	
Poecilus scitulus (LeConte)		0.1 ± 0.1			0.1 ± 0.1	
Pterostichus adstrictus (Eschscholtz)	5.3 ± 2.0	0.4 ± 0.4	0.1 ± 0.1	0.7 ± 0.4	0.1 ± 0.1	0.1 ± 0.1
Pterostichus corvinus (Dejean)	0.3 ± 0.3					
Pterostichus melanarius (Illiger)	338.6 ± 118.8	692.6 ± 224.8	27.1 ± 10.4	75.6 ± 50.4	922.0 ± 300.4	8.8 ± 4.0
Selenophorus pedicularius (Dejean)			0.1 ± 0.1			
Trachypachus inermis (Motschulsky)	0.1 ± 0.1					
Total	5545	8590	971	1140	10683	
Number of weeks sampled	10	8	8	7	8	

Values are pooled across sites and reported as mean ± SE. Beetles were identified by Rolson and McKenzie to species following Lindroth (1969).

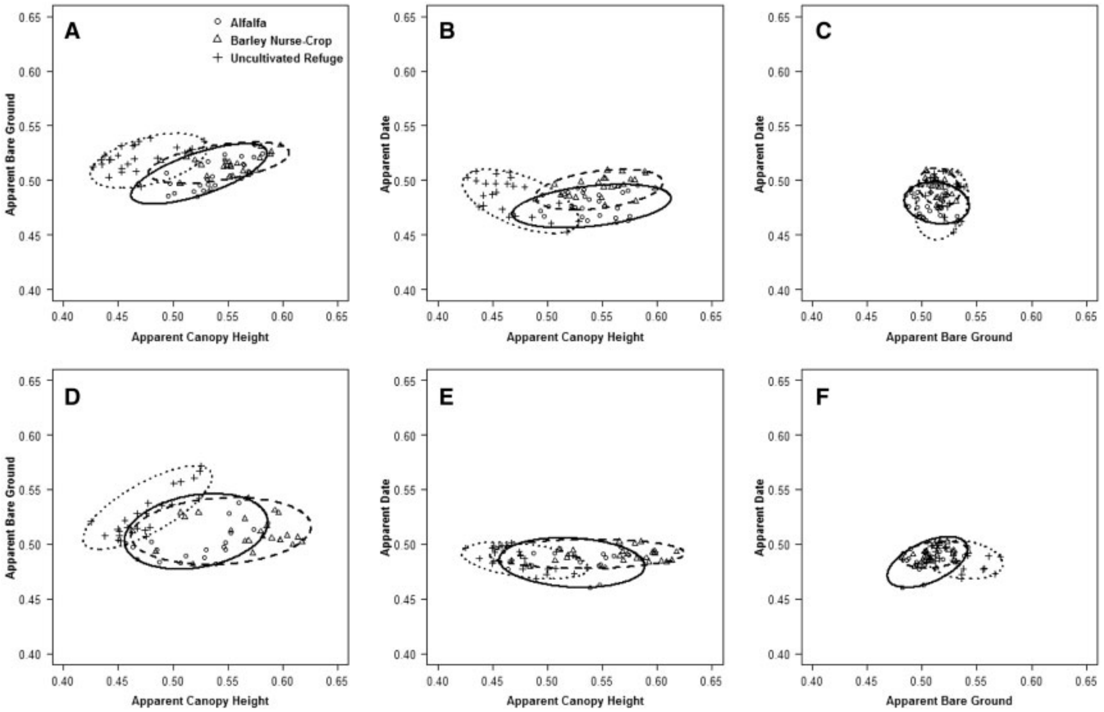

Fig. 2. Influence of canopy height, date of the growing season, and percent bare ground on carabid beetle community dynamics in monoculture alfalfa, barley nurse-crop, and uncultivated refuge fields between (A–C) May 2012 and August 2012 and (D–F) May 2013 and August 2013 at Sieban Ranch, Helena, MT. The legend in the first panel (A) also applies to all other panels (B–F). Solid ordination hulls inscribe carabid communities in monoculture alfalfa systems, dashed ordination hulls inscribe those in barley nurse-crop systems, and dotted ordination hulls inscribe those in uncultivated refuge systems.

Table 3. ANOVA table of impact of vegetation systems on carabid beetle community activity-density (natural log), species richness, and diversity at Sieban Ranch, Helena, MT

		F	df	*P*
2012	ln[Activity-Density (beetles week-1)]	11.03	2,4	0.02
	Species Richness	2.46	2,4	0.2
	α-diversity (1 − D)	4.64	2,4	0.09
2013	ln[Activity-Density (beetles week-1)]	19.53	2,4	0.01
	Species Richness	1.65	2,4	0.3
	α-diversity (1 − D)	3037	2,4	<0.001

canopy closure between monoculture alfalfa systems and uncultivated refuge areas in either year (2012: $t = 1.68$, $P = 0.09$; 2013: $t = -0.97$, $P = 0.40$).

In monoculture alfalfa systems, we found that *P. melanarius* activity-density (AD_{PTME}) was best explained by:

$$AD_{PTME} = e^{(-3.07+0.032D+0.023H)} \tag{4}$$

where D is the date of the growing season and H is the canopy height. For this species, percent bare ground was not an important predictor of AD_{PTME} in monoculture alfalfa systems after accounting for Julian date and canopy height, and was dropped from the model ($\Delta D = 35.46$; df = 47, 48; $P = 0.42$). Interestingly, canopy height, date of the growing season, and percent bare ground were not important predictors of AD_{PTME} in barley nurse crop systems ($P > 0.40$), despite the fact that AD_{PTME} was greatest in those fields. Similarly, none of these environmental variables explained AD_{PTME} in uncultivated refuge areas ($P > 0.50$).

The activity-density of *A. cupreum* (AD_{AGCU}) in monoculture alfalfa systems was best explained according to:

$$AD_{AGCU} = e^{(5.11+0.034H-0.028D+0.037B)} \tag{5}$$

where H is the canopy height, D is the Julian date, and B is the percent bare ground ($\Delta D = 253.17$; df = 47,50; $P < 0.001$). In barley nurse crop systems, canopy height, and percent bare ground were important predictors of AD_{AGCU} ($\Delta D = 386.57$; df = 45, 47; $P = 0.003$), but Julian date was not an important predictor after accounting for these two variables ($\Delta D = 0.43$; df = 44, 45; $P = 0.91$). Thus, in barley nurse crop systems, AD_{AGCU} was best predicted by:

$$AD_{AGCU} = e^{(-1.73+0.046H+0.043B)} \tag{6}$$

In uncultivated refuge areas, percent bare ground and Julian date best predicted AD_{AGCU} ($\Delta D = 16.03$; df = 45, 47; $P = 0.02$), but canopy height was not an important predictor after accounting for the other two

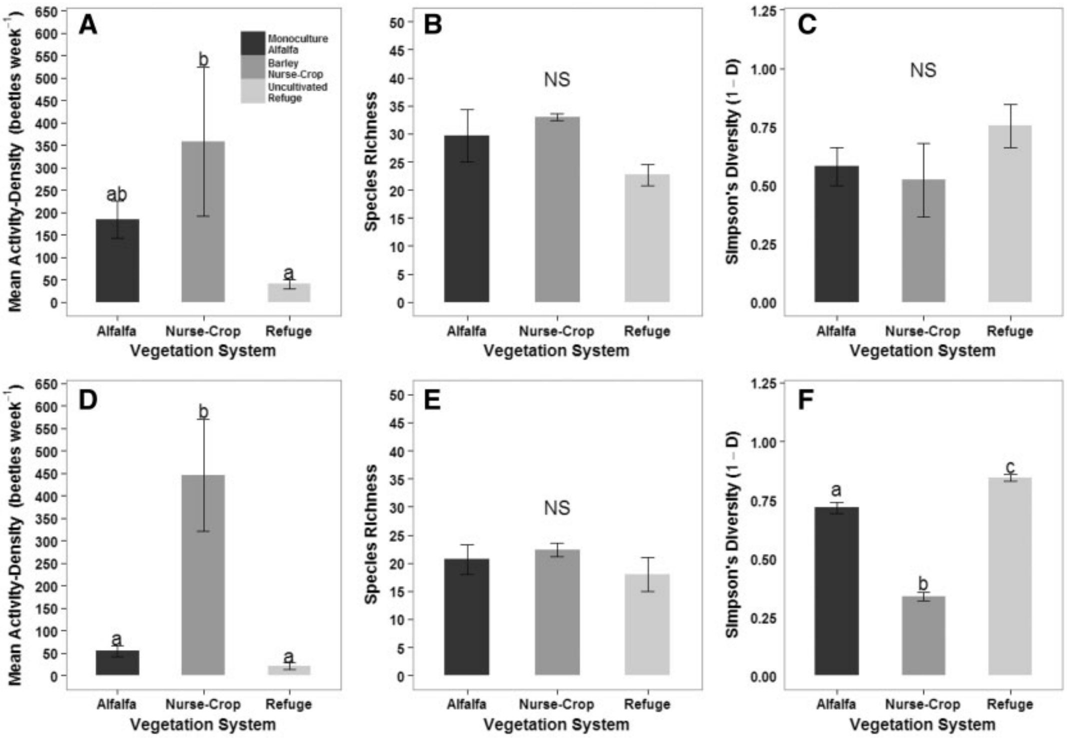

Fig. 3. Impacts of vegetation system on carabid beetle: (A) activity-density in 2012; (B) species richness in 2012; (C) α-diversity indexed by Simpson's Diversity (1–D) in 2012; (D) activity-density in 2013; (E) species richness in 2013; and (F) α-diversity in 2013 in monoculture alfalfa, barley nurse-crop, and uncultivated refuge areas at Sieban Ranch Helena, MT. Lower case letters denote means comparisons. Bars with the same lower case letters are not significantly different ($P > 0.05$). "NS" indicates that none of the means differed significantly ($P > 0.05$) from each other. The legend in the first panel (A) also applies to all other panels (B–F).

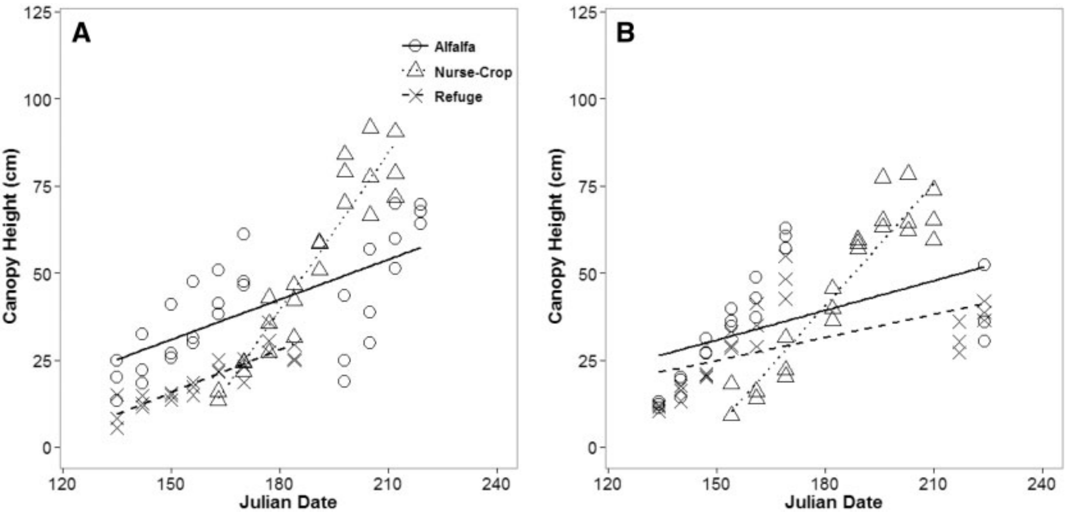

Fig. 4. Comparison of changes in canopy height during the (A) 2012 and (B) 2013 growing seasons among monoculture alfalfa, barley nurse-crop, and uncultivated refuge systems at Sieban Ranch, Helena, MT. The legend in the first panel (A) also applies to the second panel (B).

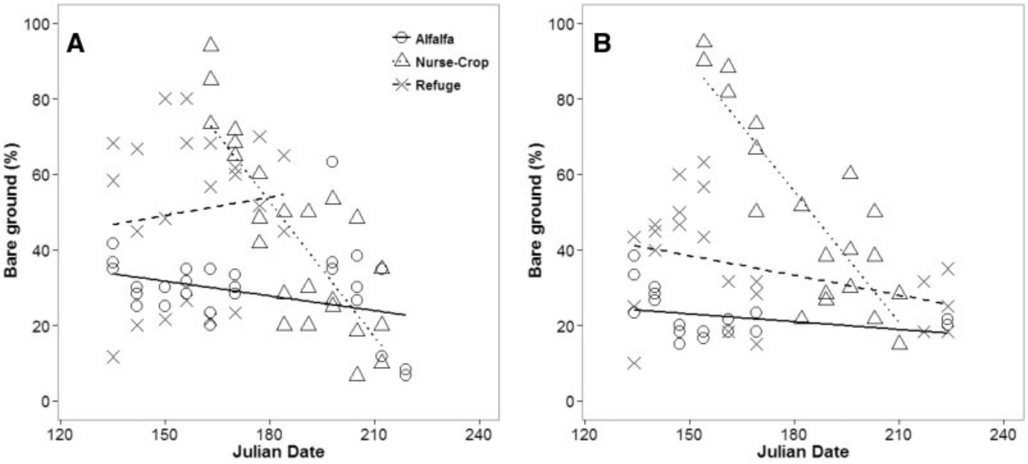

Fig. 5. Comparison of percent bare ground during the (A) 2012 and (B) 2013 growing seasons among monoculture alfalfa, barley nurse-crop, and uncultivated refuge fields at Sieban Ranch, Helena, MT. The legend in the first panel (A) also applies to the second panel (B).

variables ($\Delta D = 1.28$; df = 44, 45; $P = 0.44$). The best model for AD_{AGCU} in uncultivated refuge area was:

$$AD_{AGCU} = e^{(7.02 - 0.050B - 0.044D)} \quad (7)$$

Canopy height and percent bare ground were important predictors of *A. placidum* activity-density (AD_{AGPL}) in monoculture alfalfa systems ($\Delta D = 177.22$; df = 48, 50; $P < 0.001$), but Julian date of the growing season did not improve model fit after accounting for the other two predictors ($\Delta D = 1.29$; df = 47, 48; $P = 0.72$). Thus, the best model for the activity-density of this species was:

$$AD_{AGPL} = e^{(-1.41 + 0.050H + 0.040B)} \quad (8)$$

In barley nurse crop systems, Julian date was the best predictor of AD_{AGPL} ($\Delta D = 1875.3$; df = 46, 47; $P < 0.001$), but neither canopy height nor percent bare ground further explained AD_{AGPL} after accounting for date of the growing season. AD_{AGPL} was best predicted by:

$$AD_{AGPL} = e^{(-3.33 + 0.04D)} \quad (9)$$

A. placidum was rarely captured in uncultivated refuge areas. Accordingly, none of the measured environmental variables were important predictors of its activity-density in uncultivated refuge areas.

Discussion

In this study, we sampled a total of 64 carabid species, and in agreement with previous studies conducted in agroecosystems (Thiele 1977, Holland and Luff 2000, Luff 2002), we observed that communities were dominated by a small subset of species. Specifically, most of the sampled carabids were members of the *Amara*, *Agonum*, *Bembidion*, *Harpalus*, and *Pterostichus* genera, as is typical of temperate agricultural systems in the Northern Hemisphere (Clark et al. 1997, Petit and Usher 1998, Lee et al. 2001, Luff 2002, Gaines and Gratton 2010).

Community assembly theory predicts that a series of ecological filters selectively favors or excludes species from the regional pool in a local community (Keddy 1992, Funk et al. 2008, Myers and Harms 2009). Two local communities that share a common regional species pool, but are subjected to a different set of ecological filters, will have dissimilar community structures (Funk et al. 2008). Thus, differences in vegetative architecture, crop species, and agronomic practices can result in different carabid community structures between crop fields. Holland and Luff (2000) suggested that timing of crop husbandry, rather than the crop species identity, may be the more important filter of carabid diversity in agricultural landscapes. Nevertheless, our results suggest that vegetation type acts as an ecological filter of carabid communities as we found that species composition and community structure differed among monoculture alfalfa, barley nurse crop, and uncultivated refuge systems. Specifically, *A. placidum* and *P. melanarius* activity-densities were highest in barley nurse crop fields, but *Amara littoralis* (Dejean) and *Amara cupreolata* (Putzeys) had the lowest activity-density in those fields.

In agreement with previous research on drivers of carabid community assembly (Gardner et al. 1997, Ribera et al. 2001, Pakeman and Stockan 2014), we found that carabid community structure shifted in response to both vegetation structure and time within the growing season. Specifically, the dominant species in barley nurse crop and monoculture alfalfa systems were *P. melanarius* and *A. placidum*, both of which are polyphagous, nocturnal species (Lindroth 1969, Luff 2002, Bousquet 2012). In contrast, uncultivated refuge fields were dominated by seed predator species in the genera *Amara* and *Harpalus* (Tooley and Brust 2002).

In our study, canopy height had the strongest impact on carabid community structure. Julian date modified the effect of canopy height, but only to a small extent. Percent bare ground had a variable effect between 2012 and 2013.

Our results agree with previous observations that carabids are sensitive to the microclimate of their habitat, particularly to temperature and humidity (Thiele 1977, Evans 1983, Thomas et al. 2002). While we did not specifically measure these variables, the rate of evapotranspiration in plant communities at the stand level is proportional to green biomass (Larcher 2003), and greater vegetative cover may buffer against daily temperature fluctuation, reducing the risk of desiccation (Thomas et al. 2002). Thus, taller plant stands may be more humid, and as a result, carabid communities may shift to a composition of more hygrophilic species. By contrast, shorter plant stands may favor more xerophilious species. Alternatively, taller plant communities provide more shade, and, therefore, may increase the active period of nocturnal species (Baker and Dunning 1975, Hance 2002). Interestingly, the dynamics of the two most common species in our study suggest the latter as the dominant mechanism of community assembly. *A. placidum* is a xerophilious species, whereas *P. melanarius* is a hygrophilious species (Lindroth 1968). Yet, both species had the highest activity-densities in barley nurse crop fields, suggesting that humidity was not the major driver of habitat selection by these two dominant species. Both species, however, are nocturnal and would likely benefit from the longer active period that increased canopy height would provide (Baker and Dunning 1975, Hance 2002).

Barley nurse crop systems had greater total activity-density of carabid beetles, particularly of our two dominant species *P. melanarius* and *A. placidum*, than did monoculture alfalfa systems. This result agrees with previous research that polycultures enhance carabid populations (Kromp 1999, Holland and Luff 2000, Hance 2002). However, despite greater plant phylogenetic diversity in the uncultivated refuges, we found lower carabid activity-density in those systems than in barley nurse crop systems. This suggests that increasing plant species richness alone is not a sufficient habitat management practice for enhancing carabid populations. The structural heterogeneity hypothesis, which posits that vegetation structural heterogeneity rather than plant phylogenetic diversity is a more important factor in carabid habitat selection (Dennis et al. 1998, Siemann 1998, Brose 2003, Pakeman and Stockan 2014) helps explain the observed results. In agreement with this hypothesis, we found that the greatest carabid activity-density was in barley nurse crops, which also had the highest canopy growth and closure (as indexed by decrease in percent bare ground) rates.

Our results suggest that land managers may be able to enhance carabid species richness and total abundance by creating a heterogeneous vegetation structure, and nurse cropping may be particularly effective to achieve this goal. However, species composition is often a more important driver of ecosystem services such as biological control compared with species richness or evenness because per capita consumption rates differ among species of carabids (Straub and Snyder 2006). Thus, land managers should implement habitat management to favor a particular suite of natural enemy species rather than increasing arthropod diversity *per se* (Landis et al. 2000). Such a strategy requires predictability in the response of targeted species. Our predictive models offer strategies for targeting the most common predatory species sampled in this study.

In alfalfa, the activity-density *P. melanarius* increased with canopy height as well as Julian date, which could be explained by its autumn breeding biology and its preference for dense vegetation (Lindroth 1969). Thus, land managers seeking to conserve populations of this species, a known predator of aphids (Hemiptera:Aphidae) (Dixon and McKinlay 1992, Sunderland 2002), in monoculture alfalfa may wish to delay cutting until late in the growing season. We found the highest mean activity-density of this carabid in barley nurse crop fields. Thus, incorporating a nurse crop in production systems may be an effective strategy for increasing *P. melanarius* abundance, especially when establishing an alfalfa crop from seed.

In all three systems, we found that the activity-density of *A. cupreum*, a documented predator of cutworm eggs (Lepidoptera:Noctuidae) (Frank 1971), responded to the percent bare ground. Interestingly, *A. cupreum* activity-density increased with increasing bare ground in both monoculture alfalfa and barley nurse crop fields, but decreased with increasing bare ground in the uncultivated refuge. This suggests that *A. cupreum* does not have a monotonic response to canopy cover, but rather prefers an intermediate optimum level of canopy cover. In barley nurse crop field, the activity-density of *A. cupreum* increased with canopy height and percent bare ground. Thus, land managers may increase row spacing to enhance the abundance of this species in nurse crop fields.

Finally, the activity-density *A. placidum*, a predator of cutworm eggs (Frank 1971), increased with both increasing canopy height and bare ground in monoculture alfalfa fields. One reason that *A. placidum* may prefer both tall canopies as well as open ground is that it is a nocturnal, xerophilous species (Lindroth 1969). Open vegetation may provide more xeric conditions, but taller canopies may increase its active period (Baker and Dunning 1975, Hance 2002). In barley nurse crop fields, however, neither metric of vegetation structure was an important predictor of *A. placidum* activity-density. Thus, this species may prefer habitats of mixed grasses and legumes over plant communities with less functional diversity. A habitat management strategy for bolstering populations of *A. placidum* would thus be to plant polycultures of alfalfa and Poaceous crop species when possible. In monoculture alfalfa, land managers may wish to reduce seeding density when establishing the crop to enhance *A. placidum* populations.

In conclusion, we conducted a two-year study investigating the drivers of carabid community dynamics and the effects of vegetation structure on the habitat preferences of common carabid species under contrasting habitat management practices. Our results indicate that carabid communities vary among monoculture alfalfa, barley nurse crop, and uncultivated refuge fields. Barley nurse crop fields had greater total carabid activity-density and species richness than either of the other two systems, which suggests that nurse cropping may be an effective habitat management strategy to enhance carabid populations.

We found that carabid communities shifted in response to changes in vegetation structure. Canopy height in particular appears to be a strong driver of carabid diversity in the studied systems. Land managers seeking to enhance the populations of carabid beetles should consider changing seed row spacing or swathing dates to favor the putative habitat preferences of these species.

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