

Cover Crop Mulch and Weed Management Influence Arthropod Communities in Strip-Tilled Cabbage

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ABSTRACT Cover crop mulch and weeds create habitat complexity in agricultural fields that may influence arthropods. Under strip-tillage systems, planting rows are tilled and preestablished cover crops can remain between rows. In field experiments conducted in Michigan in 2010 and 2011, a preestablished oat (*Avena sativa* L.) cover crop was allowed to grow between rows of strip-tilled cabbage and killed at 0, 9–14, or 21–27 d after transplanting (DAT). The effects of herbicide intensity and oat kill date on arthropods, weeds, and crop yield were examined. Two levels of herbicide intensity (low or high) were used to manipulate habitat vegetational complexity, with low weed management intensity resulting in more weeds, particularly in 2010. Oat kill date manipulated the amount of cover crop mulch on the soil surface. Later oat kill dates were associated with higher natural enemy abundance. Reduced herbicide intensity was associated with 1) lower abundance of several key cabbage (*Brassica oleraceae* L.) pests, and 2) greater abundance of important natural enemy species. Habitats with both later oat kill dates and reduced herbicide intensity contained 1) fewer herbivores with chewing feeding guilds and more specialized diet breadths, and 2) greater abundance of active hunting natural enemies. Oats reduced cabbage yield when oat kill was delayed past 9–14 DAT. Yields were reduced under low herbicide intensity treatments in 2010 when weed pressure was greatest. We suspect that increased habitat complexity associated with oat mulches and reduced herbicide intensity enhances biological control in cabbage, although caution should be taken to avoid reducing yields or enhancing hyperparasitism.

KEY WORDS habitat management, herbicide, oat, herbivore, predator

Habitat management techniques that change structural and vegetational complexity in agroecosystems may affect the density of herbivores, conserve or enhance natural enemy communities, and affect predation rates of pests. Habitat complexity has been defined based on measures of nonliving and living structural complexity (Rypstra et al. 1999, Finke and Denno 2002). This includes architecture, size of nonliving structures, or both (e.g., height or biomass of dead plant material) as well as measures of living vegetational complexity including plant species diversity, height, and biomass (McNett and Rypstra 2000, Shrewsbury and Raupp 2000, Obermaier et al. 2008). Agricultural practices typically manipulate different types of complexity, primarily nonliving structural complexity and living vegetational complexity. A meta-analysis performed by Langellotto and Denno (2004) found that habitat complexity in agricultural fields increases natural enemy abundance, which can lead to greater biological control of insect pests. Several mechanisms have been proposed for this enhancement of the natural enemy community. In agro-

ecosystems, habitats with high nonliving structural complexity have been shown to provide refuge (Kawashima and Jung 2010) and vegetational complexity can provide resources for natural enemies such as shelter, pollen, and alternative prey (Root 1973, Landis et al. 2000, Sunderland and Samu 2000). Intraguild predation can also be reduced as structural and vegetational complexity is increased, enhancing biological control in greenhouses, aquatic environments, natural terrestrial habitats, and agricultural fields (Janssen et al. 2007). Habitat complexity appears to influence biological control in agricultural systems, particularly in *Brassica* crops. Increasing vegetational complexity in Chinese cabbage, broccoli, and Brussels sprouts with intercropping and living mulches increased natural enemy abundance and richness (Cai et al. 2007, Xu et al. 2011) and reduced lepidopteran and aphid pests (Costello and Altieri 1995, Vidal 1997, Hooks and Johnson 2006, Cai et al. 2007, Broad et al. 2008, Xu et al. 2011).

Other studies have demonstrated that habitat complexity negatively impacts natural enemy abundance and efficiency. For instance, structurally complex agricultural habitats negatively impacted hunting behavior or limited the ability of predators in agricultural fields, such as lady beetles, to visually search for prey (Legrand and Barbosa 2003). Abundance of *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), a

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generalist predator in corn (*Zea mays* L.) was also reduced in polycultures compared with corn monocultures (Andow and Risch 1985). Studies have demonstrated that vegetational complexity can reduce parasitoid abundance or parasitism rates through interference of visual or chemical signals from hosts in broccoli and Brussels sprouts (Costello and Altieri 1995, Smid et al. 2002). A complex habitat may change the quality of these signals, altering or reducing parasitism rates.

Managing an insect community by using behavior-modifying tools such as habitat modification of agroecosystems is challenging because the goal is to enhance crop yields, reduce pests and increase natural enemies. Rather than examining insects according to taxonomic classifications, classifying insects according to functional traits may be more informative and allow scientists to find links between groups of pests and natural enemies with changes in the habitat, allowing the conscious design of habitat management strategies. Functional traits, such as functional feeding group, feeding mode, diet breadth, and hunting mode can indicate how groups of insects within a community might respond to specific changes in the environment, or influence predation rates and herbivore abundance (Andow 1991, Harmon et al. 2003, Schmitz 2009, Szendrei and Rodriguez-Saona 2010, Woodcock and Heard 2011). This is important because generalist predators and specialized parasitoids may respond to changes in habitat structure in opposite manners. For example, Tschardt et al. (2008) demonstrated that although generalist natural enemy diversity was preserved in complex landscapes, specialized natural enemies were not, because of specific habitat or resource needs.

Growers can increase the structural and vegetational complexity in their fields through a variety of methods including intercropping (Liebman and Dyck 1993), interseeding cover crops into cash crops (Brainard et al. 2004), or planting cash crops into preestablished cover crops (Nicholson and Wien 1983). Cover crops may act as dead mulches if killed before planting, or may act as "living mulches" if allowed to grow during part or all of the crop life cycle. In strip-tillage systems, living or dead cover crop mulches can be retained between crop rows, whereas in-row areas are tilled to limit mulch interference with the crop and improve crop establishment (Luna et al. 2012). Strip-tillage in combination with cover cropping can reduce agrichemical runoff or ground water contamination, improve soil quality, protect crops and soils from extreme wind and rain events, and reduce labor and fuel inputs, ultimately improving profitability although protecting the environment (Luna and Staben 2002, Potter et al. 2008, Mulvaney et al. 2011, Brainard and Noyes 2012, Luna et al. 2012).

In vegetable crops, both living and dead mulch systems have shown beneficial effects for reducing insect pests (Altieri et al. 1985) and suppressing weeds (Liebman and Dyck 1993, Teasdale 1998). For example, in cereal crops, predation rates of major pests were highest in the presence of cover crop mulch (Schmidt et al. 2004, Lundgren and Fergen 2010). The

impact of cover crop mulches on arthropod communities in cabbage (*Brassica oleraceae* L.) is not well understood, although the impact of cover crop mulches on pest populations, particularly Lepidoptera, has been well studied in other *Brassica* crops such as broccoli (Mangan et al. 1995).

Although cover crop mulch systems have shown benefits for weed and insect suppression, these benefits have often come at the expense of crop yields, because of competition for nutrients, water, or light (Teasdale 1998, Brainard and Bellinder 2004). One approach for minimizing interference between living mulches and crops is to kill mulches before the crop has reached the "critical weed free period" (CWFP) (Muller-Scharer and Potter 1991). In weed management studies, the CWFP is defined as the period during which weeds must be removed to avoid yield loss (Martin et al. 2001). For transplanted cabbage, CWFP studies (Weaver 1984) suggest that cover crops must be terminated within 3–4 wk of transplanting to avoid yield losses. However, CWFP vary considerably with environmental conditions and weed (or cover crop) species and density (Weaver et al. 1992), so the critical period of removal for preestablished cover crop mulches is not well established.

Growers using habitat management strategies such as cover crop mulch may also be able to reduce herbicide inputs in their fields based on weed suppressive effects of cover crop mulches. Combining cover crop mulches and reduced herbicide inputs can increase the habitat complexity between rows. In a variety of fruit crops and field corn, increasing noncrop species was associated with increases in natural enemy abundance and reductions in pest populations (Rieux et al. 1999, Letourneau et al. 2011). Increased weed diversity also reduced pest populations in beans (Andow 1990, Andow 1992), and increased generalist predator abundance in other vegetable crops, such as collards, corn, cauliflower, and tomato (*Solanum lycopersicum* L.) (Altieri et al. 1985, Schellhorn and Sork 1997). Predation of a common herbivore in beans also increased in weedy plots (Andow 1990). However, weed diversity had little impact on predation by generalist predators in field corn (Wilson et al. 2004) and reduced specialized natural enemy populations in canola (*Brassica napus* L., *Brassica rapa* L.) (Broatch et al. 2010). In addition, beneficial effects of weeds on arthropod communities must be weighed against potential negative effects on crop quality and yield that often are associated with low herbicide intensity.

Typical pests in cabbage fields in North America consist of specialized *Brassica* feeders, including the cabbage aphid, *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae); imported cabbageworm, *Pieris rapae* (L.) (Lepidoptera: Pieridae); and diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) (Root 1973). An oligophagous cabbage pest, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae) and two generalist herbivores, the cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), and onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), are also of economic importance throughout the United

States (Hines and Hutchison 2001, Shelton et al. 2008). Specialized natural enemies, such as the parasitic wasps *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae) and *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), and generalist predators (e.g., spiders, carabids, harvestmen, lady beetles, and predatory stinkbugs) attack these pests. The natural enemy community in Michigan cabbage fields consists of the spined soldier bug [*Podisus maculiventris* (Say)] (Hemiptera: Pentatomidae), minute pirate bug [*Orius tricolor* (White)] (Hemiptera: Anthracoridae), and predatory thrips (*Aelothrips* sp., Thysanoptera: Aeolothripidae). Lady beetle species are dominant predators, primarily the lady beetle *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae), *Propylaea quatuordecimpunctata* (L.) (Coleoptera: Coccinellidae), *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), and convergent lady beetle [*Hippodamia convergens* (Guerin-Méneville)] (Coleoptera: Coccinellidae).

Habitat management techniques, such as flowering strips (Piffner et al. 2009) and companion plants (Hooks and Johnson 2003) have been studied to enhance biological control of cabbage pests and populations of these natural enemies. However, it is unknown how levels of mulch and herbicide intensity may influence community structure and abundance of herbivores and natural enemies in this system.

The primary objective of this study was to examine the impact of increasing both components of habitat complexity: structural and vegetational complexity between rows, on herbivore and natural enemy communities and crop yield in cabbage. An oat (*Avena sativa* L.) cover crop killed at different dates in the spring was used to manipulate the amount of physical structure between rows—the structural complexity within the habitat. Earlier kill dates translated to less physical structure as the oat cover crop was smaller when it was terminated, whereas at the latest kill date, oats were much taller and created more structural complexity. The use of high or low herbicide intensity created different levels of weed biomass, or vegetational complexity. For the purpose of this study, structural complexity refers to the amount of oat mulch in the row middle, as determined by oat kill date. Vegetational complexity refers to the amount of weed biomass, manipulated by herbicide intensity. We determined whether higher structural and vegetational complexity influenced arthropod community structure, functional groups, and species abundance. The secondary objective was to assess the impact of oat kill date and herbicide intensity on weed suppression.

Materials and Methods

Experimental Design. We performed a field study at Michigan State University's Horticulture Farm in East Lansing, MI. In 2010 and 2011, separate fields were used, both with Marlette fine sandy loam soil. The experimental design in both years was a randomized complete block design with 6 treatments and 4 replications. Treatments were a combination of two main effects: oat kill date (early, intermediate, or late)

Table 1. Dates of major field operations in 2010 and 2011

Field operation	Date	
	2010	2011
Oats planted	14 April	14 April
Strip-tillage	20-May	24 May
Oxyfluorfen/Dual II Magnum applied	20-May	24 May
Clethodim applied in early oat kill	20-May	24 May
Cabbage transplanted	21-May	31 May
Clethodim applied in intermediate oat kill	14 June	9 June
Clethodim applied in late oat kill	17 June	21 June
Oxyfluorfen applied in high herbicide intensity	11 June	NA
Urea sidedress application	22 June	27 June
Hand weeding	21 June	29 June
Hand weeding 2 in high herbicide intensity	NA	10 Aug.
Cabbage harvest	17 Aug.	8 Sept.

and herbicide intensity (low or high). Low herbicide intensity treatments received standard cabbage preemergence herbicides. High herbicide intensity treatments received preemergence herbicides and either an additional postemergence herbicide (2010) or supplemental hand weeding (2011) to effectively exclude all weeds. In 2010, plots were 3.0 by 7.6 m, with four rows of cabbage spaced 76 cm apart. In 2011, plot size was increased to 4.6 by 9.1 m with six rows of cabbage per plot.

Field Operations. The dates of major field operations are provided in Table 1. In mid-April the entire experimental area was fertilized with 91 kg/ha of 19-19-19 (N-P-K), and oats (*Avena sativa* variety 'Ida'; Zmitko Farm, Owosso, MI) were planted using a grain drill (Great Plains Compact Drill 3P606NT, Salina, KS). Oats were sown at 126 kg/ha in 2010, and at 175 kg/ha in 2011. In late May, an additional 228 kg/ha of 19-19-19 (N-P-K) fertilizer was applied over the entire experimental area in accordance with soil tests and nutrient management recommendations for cabbage (Warncke et al. 2004). A Hiniker model 6000 two-row strip-tiller (Hiniker Company, Mankato, MN) (equipped with notched trash-cleaning discs, cutting-coulter, shank-point assembly, berming disks, and rolling basket) was used to create 25- by 25-cm deep strips at 76 cm between-strip spacing. Preestablished oats were effectively killed in the strips, but minimally affected in the undisturbed 51 cm between strips, thus creating a cover crop mulch between crop rows. After strip-tillage, a pretransplant herbicide application containing Goal (Dow AgroSciences, Indianapolis, IN) (0.28 kg active ingredient oxyfluorfen/ha) and Dual II Magnum (Syngenta, Guelph, Ontario, Canada) (0.54 kg active ingredient s-metolachlor/ha) was applied in all treatments. For early oat kill-date treatments, Select 2 EC (0.21 kg active ingredient clethodim/ha) also was applied at this time. Intermediate oat kill treatments with Select EC (Winfield Solutions LLC., Saint Paul, MN) occurred 14 d after transplanting (DAT) in 2010, and 9 DAT in 2011. Late oat kill treatments occurred 27 DAT in 2010 and 21 DAT in 2011. In 2010, high herbicide intensity plots received a postemergence herbicide application to manage broadleaf weeds 28 DAT (Goal, 0.28-kg active ingredient oxyfluorfen/ha); these plots also were

hand-weeded 31 DAT. Because of reduced weed pressure in 2011, no additional postemergence herbicides were applied in high herbicide intensity plots, although plots were hand-weeded at 29 and 71 DAT to remove escaped weeds.

Cabbage transplants (variety 'Blue Dynasty'; Siegers Seed Company, Holland, MI) were grown to the 4–6 leaf stage in 98 cell plug trays and hardened off for either 4 d (2010) or 14 d (2011) before transplanting in the field. Cabbage was transplanted by hand on 21 May 2010 and 31 May 2011 into strip-tilled zones (76 cm between rows) with 36 cm between transplants within the row. No fungicides were used. In 2011, an insecticide selective for lepidopteran pests, Intrepid (0.56 kg active ingredient methoxyfenozide/ha), was applied when imported cabbageworm damage became severe 43 DAT. Cabbage was side-dressed with urea at 45 kg N/ha on 22 June 2010 and 27 June 2011.

Oat Height and Biomass. In 2010, we measured oat height in two 0.25-m² quadrats randomly placed in each plot. The heights of 10 random oat plants per 0.25-m² quadrat were measured before cabbage transplant and 10, 26, and 52 DAT in all plots. During the final height measurements, one quadrat of dead oat biomass was collected per plot to determine oat dry weight. Above ground oat biomass was dried in the oven for 7 d at 60°C before weighing. In 2011, oat height was measured using the same methods as 2010. However, we recorded oat height in intermediate, late, and all treatments 9, 16, and 46 DAT, respectively. Killed oat biomass in 2011 was collected from one 0.25-m² quadrat per plot at nine and 17 DAT, in intermediate and late kill date plots, respectively. Oats were not present at these dates in early kill date plots.

Weed biomass. A weed census was conducted at the end of the cabbage growing season in 2010, 84 DAT. Two weed species, common lambsquarters (*Chenopodium album* L.) and smartweed (*Polygonum pensylvanicum* L.), dominated the weed community. In two 0.25-m² quadrats per plot, lambsquarter and smartweed biomass was collected, dried, and weighed as described previously for oats. In 2011, a weed census was conducted 45, 84, and 90 DAT. Compared with 2010, weed density was lower in low herbicide intensity treatments, but a more diverse weed community was present including, in order of abundance: common lambsquarters, common ragweed (*Ambrosia artemisiifolia* L.), fall panicum (*Panicum dichotomiflorum* Michx.), and wild radish (*Raphanus raphanistrum* L.). Weed biomass was collected for common lambsquarters and common ragweed (>95% of total weed biomass) from four 0.25-m² quadrats in each plot. A larger sampling area was used in 2011 because weed density was lower in 2011 compared with 2010.

Cabbage Biomass and Yield. To determine midseason cabbage plant biomass, we randomly collected four cabbage plants per plot 40–46 DAT in 2010 and 27 DAT in 2011. Cabbage plants were cut above the root crown, washed, and weighed. The numbers of leaves per plant were counted and total leaf area was measured (Portable Leaf Area Meter LI-3000C 1.0.0, LI-COR Biosciences, Lincoln, NE). For final cabbage

yield, on 17 August 2010, all cabbage heads were harvested from the middle 7-m sections of the two center rows for each cabbage plot. Final cabbage yield in 2011 was taken on 8 September 2011 from the middle 4.6-m sections of the center four rows of each plot. In both years, the number and weight of marketable and non-marketable heads were assessed, with those >11.4 cm in diameter classified as marketable.

Habitat and Cabbage Yield Statistical Analysis. The effects of oat kill date and herbicide intensity on oat height, oat biomass, weed biomass, cabbage biomass (marketable and nonmarketable), cabbage leaf area, and number of cabbage leaves per plant were assessed using a mixed model (PROC Mixed, SAS 9.2, SAS Institute 2002–2008) with herbicide intensity and oat kill date as fixed factors, and block as a random factor. Oat height was averaged across three sampling dates. Oat biomass and weed biomass were summed for each plot. Oat biomass was log transformed ($x + 0.5$) to meet assumptions of normality and equal variance. The other dependent variables were tested and transformations were not necessary. A least-square means test was performed if main effects or their interactions were significant (at $\alpha = 0.05$). For each dependent variable, the 2 yr were analyzed separately.

Insect Community Assessment. Insects were sampled visually and with yellow sticky traps (7.5 by 12.3 cm, Great Lakes Integrated Pest Management [IPM], Vestaburg, MI) in the growing season for 9 wk in 2010 and 14 wk in 2011. Sessile insects were measured visually once a week on 10 randomly sampled cabbage plants per plot in the center cabbage rows. All cabbage leaves were examined and insects on them were identified and counted. Mobile or flying insects were sampled using yellow sticky traps placed 0.4 m from ground level on metal stakes. Traps were changed weekly and insects were identified to species or to the lowest possible taxonomic classification (Marshall 2006). Voucher specimens for the imported cabbageworm, diamondback moth, and representatives of the natural enemy community were deposited in the A.J. Cook Arthropod Research Collection at Michigan State University (East Lansing, MI).

To determine the impact of our treatments on insect community structure, we performed cluster analysis (PROC Cluster). Average abundance per treatment of each insect species was used to conduct the analysis. Herbivores and natural enemies were analyzed separately in both years. This type of cluster analysis uses average linkage distance to determine similarity between groups. Data from visual sampling and sticky traps was transformed using $\log(x + 0.01)$ and analyzed separately for 2010 and 2011. A repeated measures analysis was used, with date as a repeated factor, block as a random factor, and treatment nested within block as the subject. Fixed factors included herbicide intensity, oat kill date, and interaction between herbicide intensity and oat kill date (PROC Mixed). If main effects were significant ($\alpha = 0.05$), we performed least-square means tests with Tukey–Kramer adjustment.

To identify how the herbicide intensity and oat kill date treatments influenced functional groups of nat-

Table 2. Mean ± SEM oat height (ht), oat biomass, and weed biomass in 2010 and 2011

Main effects	Oat ht (cm) ^{a,b}		Oat biomass (g/m ²) ^{a,c}		Weed biomass (g/m ²) ^a	
	2010	2011	2010	2011	2010	2011
Oat kill date						
Early	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	0.0 ± 0.0a	167.28 ± 83.09	9.03 ± 5.92
Intermediate	8.21 ± 0.51b	41.67 ± 0.93b	NA	28.21 ± 5.66b	131.21 ± 51.96	34.15 ± 15.79
Late	26.75 ± 0.72c	46.56 ± 1.53c	173.63 ± 13.61b	87.06 ± 8.40c	104.23 ± 46.68	10.39 ± 8.47
Herbicide intensity						
Low	11.11 ± 3.17a	29.58 ± 6.36	53.67 ± 23.51	39.59 ± 12.25	266.26 ± 44.16a	35.71 ± 10.83a
High	12.19 ± 3.60b	29.24 ± 6.34	62.08 ± 27.22	37.26 ± 11.51	2.22 ± 1.08b	0.0 ± 0.0b
Significance			<i>P</i> value			
Oat kill date (KD)	<0.01	<0.01	<0.01	<0.01	0.49	0.06
Herbicide intensity (HI)	<0.01	0.79	0.39	0.74	<0.01	<0.01
KD × HI	<0.01	0.77	0.47	0.84	0.49	0.06

^a Different letters within column indicate significant differences within main effects according to LSM means ($\alpha = 0.05$).

^b These represent average heights during the 2010 or 2011 season.

^c These represent maximum weights during the 2010 or 2011 season.

ural enemies and herbivores, we calculated Hedge’s D effect size (Cohen 1988) by using Metawin 2.0 (Sinaur Associates, Sunderland, MA). A positive or negative effect size indicates a positive or negative impact of habitat complexity on insect abundance. Any confidence interval overlapping with zero indicates a lack of significant difference between the lowest and highest complexity habitats for that functional group. Insect species from visual and sticky trap sampling were categorized as herbivore, predator, or parasitoid, and according to feeding guild (chewing, sucking, none), hunting mode (active or sit and wait), and diet breadth (specialist, generalist, oligophagous) (specialists: herbivores with hosts within a single plant family, oligophagous: herbivores with hosts in two plant families, generalists: herbivores with hosts in more than two plant families) (Supplemental Table S1). Effect size was used to compare the effects of our two extreme treatments (high herbicide intensity and early oat kill date, compared with low herbicide intensity and late oat kill date) (Cohen 1988, Horton et al. 2003). These two extreme treatments will be referred to as the lowest habitat complexity and highest habitat complexity treatments from here on. For less mobile herbivores that often concentrated on their food source, visually collected insect abundance data from these two treatments was used to calculate average herbivore species’ abundance per plot for each week. Sticky trap data from these two treatments were used to calculate average natural enemy species abundance and mobile herbivore abundance per plot per week. Our analysis used a fixed effects model with categorical structure and included resampling tests (999 iterations) that calculate cumulative effect size with 95% confidence intervals. Mean effect size (d+) and 95% bootstrap confidence intervals were calculated for each feeding category (Gurevitch and Hedges 1999). Effect sizes of 0.2, 0.5, and 0.8 are considered small, intermediate, and large, respectively (Cohen 1988). To determine significance, between-group heterogeneity (Q_b) was considered with a chi-square distribution.

Results

Oat Height and Biomass. In 2010, killed oat height was affected by oat kill date, herbicide intensity, and their interaction (Table 2). Within low and high herbicide intensity plots, oats were more than three times taller in late-killed oats, compared with the intermediate-killed plots ($t > 27.35$, $df = 15$, $P < 0.01$). In 2011, oat height did not differ across plots with different herbicide intensity, but oat height was different among plots with different oat kill dates. Plots with a late kill date had 10% taller oats than the intermediate kill date plots ($t = 3.15$, $df = 18$, $P < 0.01$).

In both years, oat biomass was influenced by oat kill date but not herbicide intensity (Table 2). In 2010, late killed oats produced 173.63 g/m² of biomass after termination, whereas early killed oats did not produce substantial oat biomass, because these decayed before the sampling date. In 2011, three times more biomass was produced in late killed oats than intermediate killed oats ($t = 3.15$, $df = 15$, $P < 0.01$). Both late and intermediate killed oats produced greater biomass than early killed oats ($t > 26.77$, $df = 15$, $P < 0.01$).

Weed Biomass. In both years, weed biomass was affected by herbicide intensity but not by oat kill date (Table 2). In 2010, low herbicide intensity plots produced 266 g/m² biomass compared with only 2 g/m² in high herbicide intensity plots ($t = 6.24$, $df = 15$, $P < 0.01$). In 2011, weed biomass was far lower than in 2010, with greater biomass in low- compared with high-intensity herbicide plots. We had anticipated that oat mulch might provide weed suppressive benefits through shading or competition for water or nutrients. However, no such effect was detected, likely due in part to large within-treatment variability in weed biomass.

Cabbage Biomass and Yield. Mid-season cabbage biomass and leaf area per plant were affected by oat kill date but not by herbicide intensity in 2010 (Supplemental Table S2). Cabbage leaf area in early and intermediate kill-date plots did not differ, but leaves were 36% greater in late kill-date plots. Early and intermediate kill date plots also had 36–64% greater midseason cabbage biomass than late kill date plots.

Table 3. Mean ± SEM non-marketable and marketable fresh weight of cabbage heads in 2010 and 2011

Main effects	Marketable (kg) ^a		Nonmarketable (kg) ^a	
	2010	2011	2010	2011
Oat kill date				
Early	48.51 ± 3.54a	60.31 ± 6.37a	0.36 ± 0.14a	2.37 ± 0.69
Intermediate	40.86 ± 4.20a	50.20 ± 7.28ab	1.83 ± 0.77ab	3.56 ± 1.29
Late	24.84 ± 4.44b	38.51 ± 4.27b	2.86 ± 0.74b	4.03 ± 0.82
Herbicide intensity				
Low	32.65 ± 4.11a	46.09 ± 5.29	1.36 ± 0.49	3.73 ± 0.68
High	43.49 ± 4.08b	53.25 ± 5.61	2.01 ± 0.65	2.91 ± 0.89
Significance		<i>P</i> value		
Oat kill date (KD)	<0.01	0.02	0.03	0.38
Herbicide intensity (HI)	<0.01	0.21	0.35	0.42
KD × HI	0.70	0.83	0.83	0.65

^a Different letters within column indicate significant differences within main effects according to LSM means ($\alpha = 0.05$).

Although the leaf area per cabbage plant differed across oat kill date, the number of cabbage leaves per plant did not (Supplemental Table S2; $F = 0.84$; $df = 2,15$; $P = 0.45$). In 2011, midseason cabbage biomass, leaf area, and number of leaves did not differ across oat kill date or herbicide intensity ($F < 1.89$; $df = 2,15$; $P > 0.19$; Supplemental Table S2). This discrepancy between years may have been due in part to the fact that cabbage was sampled at a later date in 2010 compared with 2011, so greater interference from oats may have occurred by the time of sampling. Oat biomass in late kill date treatments was also lower in 2011 (Table 2), because of a slightly earlier kill date relative to cabbage transplanting.

The final yield (Table 3) and number of marketable and nonmarketable cabbage (Supp Table S3) in 2010, was affected by oat kill date. Marketable cabbage biomass was two times greater in early compared with late kill date plots ($t = 5.43$, $df = 15$, $P < 0.01$) and 64% greater in intermediate kill date plots ($t = 1.75$, $df = 15$, $P = 0.1$). Early kill date plots had 37% more marketable heads than late kill date plots ($t = 3.39$, $df = 15$, $P < 0.01$) and intermediate kill date plots had marginally more marketable heads (23%) than late kill date plots ($t = 2.10$, $df = 15$, $P = 0.05$). Nonmarketable heads were more abundant in late kill date plots compared with plots with oats killed at an early ($t = 3.58$, $df = 15$, $P < 0.01$) or intermediate date ($t = 2.21$, $df = 15$, $P = 0.04$).

In 2011, marketable cabbage yield was 57% higher in early compared with late kill date plots ($t = 3.24$, $df = 15$, $P < 0.01$; Table 3). Nonmarketable yield and the number of marketable or nonmarketable cabbage heads per plot in 2011 were not different across herbicide intensity ($F < 1.66$; $df = 1,15$; $P > 0.21$; Table 3, Supplemental Table S3) or oat kill date treatments ($F < 2.65$; $df = 2,15$; $P > 0.10$).

Herbicide intensity affected marketable yield and number in 2010, but had no effect on final yield or number in 2011 (Table 3, Supplemental Table S3). In 2010, marketable cabbage weight was reduced by 33% under low compared with high herbicide intensity treatments ($t = 3.04$, $P < 0.01$). Greater yield loss because of weeds in 2010 was likely the result of greater weed biomass in 2010 compared with 2011 (Table 2).

Insect Community Structure. In 2010, there were two distinct herbivore communities according to her-

bicide intensity (Fig. 1A). Herbivore communities were more similar between plots where oats were killed at an intermediate or later date compared with plots where oats were killed early in the season. In 2011, herbivore communities were similar in treatments where oats were killed late in the season, irrespective of herbicide intensity. The herbivore communities in plots

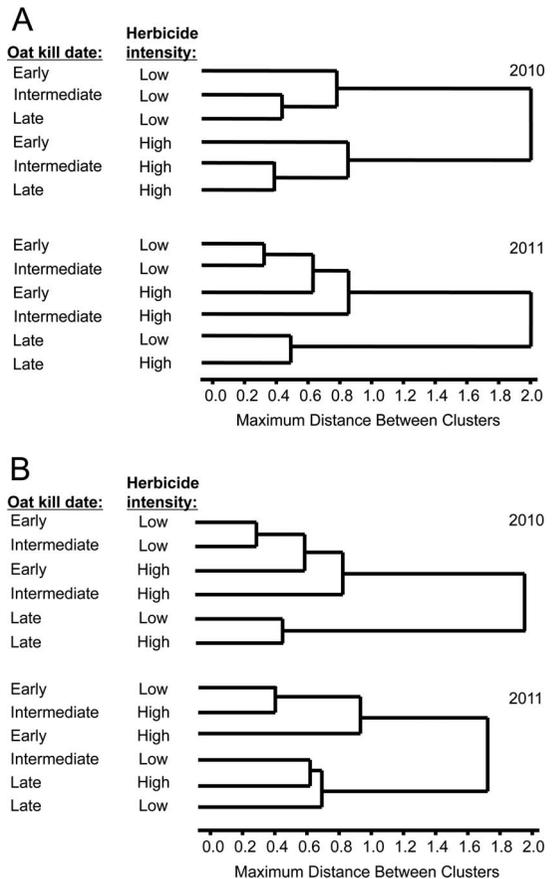


Fig. 1. Habitat complexity dendrograms based on average linkage distance for the herbivore community (A) and natural enemy community (B) in 2010 and 2011.

Table 4. Mean ± SEM herbivore abundance in experimental plots across fixed effect: oat kill date (early, intermediate, or late) in 2010 and 2011

	Insect abundance (mean ± SEM) ^a			Source of variation		
	Early oat kill date plots	Intermediate oat kill date plots	Late oat kill date plots	Oat kill date		
				df ^b	F	P
2010 major herbivores						
Imported cabbageworm ^c	5.45 ± 0.51	9.19 ± 1.23	8.48 ± 2.19	2,53	3.15	0.05
Diamondback moth ^c	16.32 ± 1.64	14.97 ± 2.07	16.81 ± 3.88	2,55	0.99	0.38
Cabbage looper ^c	4.14 ± 0.70a	7.64 ± 1.43b	7.38 ± 2.33ab	2,19	4.72	0.02
Cabbage aphid ^d	37.08 ± 4.05	35.16 ± 4.30	27.66 ± 3.68	2,14	1.21	0.33
<i>Phyllotreta cruciferae</i> ^d	18.60 ± 2.32	17.19 ± 2.28	23.51 ± 3.08	2,15	1.37	0.28
Onion thrips ^d	55.00 ± 5.07	67.32 ± 7.85	49.21 ± 4.49	2,15	1.40	0.28
2011 major herbivores						
Imported cabbageworm ^c	12.53 ± 1.42	13.00 ± 1.42	13.02 ± 1.60	2,15	0.15	0.87
Diamondback moth ^c	2.82 ± 0.35	2.23 ± 0.29	2.09 ± 0.30	2,18	2.60	0.10
Cabbage looper ^c	0.08 ± 0.04	0.05 ± 0.04	0.04 ± 0.03	2,18	1.09	0.36
Cabbage aphid ^d	63.56 ± 12.42	63.44 ± 12.08	72.50 ± 15.93	2,15	1.60	0.23
<i>Phyllotreta cruciferae</i> ^d	76.53 ± 14.68	77.81 ± 18.06	75.10 ± 19.87	2,15	1.44	0.27
Onion thrips ^d	50.84 ± 4.41	79.81 ± 8.03	73.95 ± 7.04	2,72	2.76	0.07

^a Different letters indicate significant differences within row according to LSMeans ($\alpha = 0.05$).

^b Denominator degrees of freedom were calculated with the Kenward-Roger method (SAS 9.2, 2002–2008).

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

with an early or intermediate oat kill date were similar within the plots with low herbicide intensity.

In 2010, the natural enemy communities were similar in late oat kill date plots regardless of herbicide intensity (Fig. 1B). There were distinct natural enemy communities in early or intermediate oat kill date plots with the two different herbicide intensities. The natural enemy communities within early and intermediate kill date treatments were particularly similar across low herbicide intensity. In 2011, the natural enemy communities were similar in early and intermediate kill date treatments, but the communities within plots with an intermediate kill date and low herbicide intensity were more similar to the communities found where oats were killed later in the season.

Insect Abundance. Because interactions between main effects were not significant for insect abundance,

we present only the results for main effects. A few herbivore and natural enemy species consistently did not respond to experimental treatments in 2010 or 2011. Abundance of herbivores such as the diamondback moth, onion thrips, and *Phyllotreta cruciferae* were not different among any of our oat kill date (Table 4) or herbicide intensity treatments (Table 5). Abundance of a natural enemy, *Harmonia axyridis*, was also not different across oat kill date (Table 6) or herbicide intensity (Table 7). In addition, the abundance of the braconid wasp *Cotesia rubecula*, a specialist parasitoid that attacks the imported cabbageworm, was not significantly different among treatments in either 2010 or 2011.

Impact of Oat Kill Date on Insect Abundance. Oat kill date had a marginal impact on herbivore abundance; for example, the imported cabbageworm lar-

Table 5. Mean ± SEM herbivore abundance in experimental plots across fixed effect: herbicide intensity (low or high) in 2010 and 2011

	Insect abundance (mean ± SEM) ^a		Source of variation		
	Low herbicide intensity plots	High herbicide intensity plots	Herbicide intensity		
			df ^b	F	P
2010 major herbivores					
Imported cabbageworm ^c	7.29 ± 0.83	8.10 ± 1.50	1,53	0.10	0.75
Diamondback moth ^c	15.49 ± 1.63	16.59 ± 2.65	1,55	0.53	0.47
Cabbage looper ^c	5.35 ± 0.98a	7.41 ± 1.60b	1,19	5.88	0.03
Cabbage aphid ^d	17.34 ± 1.62a	49.05 ± 3.78b	1,14	60.95	<0.01
<i>Phyllotreta cruciferae</i> ^d	16.61 ± 1.63	22.81 ± 2.46	1,15	0.04	0.83
Onion thrips ^d	56.68 ± 5.64	57.83 ± 4.19	1,15	0.18	0.67
2011 major herbivores					
Imported cabbageworm ^c	11.70 ± 1.12a	14.00 ± 1.29b	1,15	5.37	0.04
Diamondback moth ^c	2.36 ± 0.27	2.40 ± 0.25	1,18	1.56	0.23
Cabbage looper ^c	0.09 ± 0.04	0.02 ± 0.01	1,18	3.75	0.07
Cabbage aphid ^d	58.23 ± 8.71a	74.77 ± 12.98b	1,15	9.93	<0.01
<i>Phyllotreta cruciferae</i> ^d	70.61 ± 13.93	82.36 ± 14.84	1,32	0.39	0.54
Onion thrips ^d	70.92 ± 5.56	65.48 ± 5.52	1,72	0.24	0.63

^a Different letters indicate significant differences within row according to LSMeans ($\alpha = 0.05$).

^b Denominator degrees of freedom were calculated with the Kenward-Roger method (SAS 9.2, 2002–2008).

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

Table 6. Mean \pm SEM natural enemy abundance in experimental plots across fixed effect: oat kill date (early, intermediate, or late) in 2010 and 2011

	Insect abundance (mean \pm SEM) ^a			Source of variation		
	Early oat kill date plots	Intermediate oat kill date plots	Late oat kill date plots	Oat kill date		
				df ^b	F	P
2010 major natural enemies						
Spined soldier bug ^c	1.20 \pm 0.62	2.71 \pm 0.98	1.36 \pm 0.39	2,19	1.20	0.32
<i>Coleomegilla maculata</i> ^c	0.97 \pm 0.16	0.78 \pm 0.13	1.30 \pm 0.19	2,15	3.48	0.06
<i>Propylea quatuordecimpunctata</i> ^c	0.46 \pm 0.10	0.67 \pm 0.13	0.76 \pm 0.13	2,15	1.39	0.28
<i>Harmonia axyridis</i> ^c	0.07 \pm 0.03	0.05 \pm 0.03	0.06 \pm 0.03	2,20	0.23	0.80
Lady beetle larvae ^d	0.34 \pm 0.12a	0.33 \pm 0.13a	0.96 \pm 0.24b	2,15	4.26	0.03
Minute pirate bug ^c	5.40 \pm 0.89	4.27 \pm 0.72	3.21 \pm 0.58	2,19	1.74	0.20
Predatory thrips ^c	18.03 \pm 2.12	19.34 \pm 2.70	11.14 \pm 1.63	2,15	1.24	0.32
<i>Cotesia rubecula</i> ^c	10.78 \pm 2.03	6.30 \pm 1.21	6.51 \pm 1.30	2,18	1.56	0.24
Chalcidoidea ^c	23.78 \pm 1.60a	28.37 \pm 1.74b	37.82 \pm 2.04c	2,15	24.39	<0.01
2011 major natural enemies						
Spined soldier bug ^c	0.64 \pm 0.29	0.45 \pm 0.24	0.63 \pm 0.38	2,19	0.05	0.95
<i>Coleomegilla maculata</i> ^c	0.76 \pm 0.11	1.20 \pm 0.17	1.51 \pm 0.18	2,15	2.00	0.17
<i>Propylea quatuordecimpunctata</i> ^c	0.05 \pm 0.02a	0.14 \pm 0.04ab	0.22 \pm 0.06b	2,15	3.88	0.04
Convergent lady beetle ^c	0.11 \pm 0.03ab	0.39 \pm 0.09a	0.09 \pm 0.03b	2,21	3.53	0.05
<i>Harmonia axyridis</i> ^c	0.02 \pm 0.02	0.07 \pm 0.03	0.00 \pm 0.00	2,15	2.21	0.14
Lady beetle larvae ^d	0.08 \pm 0.03a	0.19 \pm 0.06ab	0.38 \pm 0.12b	2,114	5.96	<0.01
Minute pirate bug ^c	0.84 \pm 0.14	1.63 \pm 0.29	1.50 \pm 0.23	2,18	1.78	0.20
Predatory thrips ^c	2.48 \pm 0.33a	3.10 \pm 0.42ab	3.06 \pm 0.40b	2,15	3.63	0.05
<i>Cotesia rubecula</i> ^c	1.30 \pm 0.26	1.32 \pm 0.27	1.70 \pm 0.39	2,19	1.18	0.33
<i>Diadegma insulare</i> ^c	4.02 \pm 0.94a	2.48 \pm 0.71b	2.42 \pm 0.77b	2,15	4.54	0.03
Chalcidoidea ^c	17.31 \pm 1.09a	21.33 \pm 1.46b	31.88 \pm 3.27c	2,19	9.15	<0.01

^a Different letters indicate significant differences within row according to LSMeans ($\alpha = 0.05$).

^b Denominator degrees of freedom were calculated with the Kenward-Roger method (SAS 9.2, 2002–2008).

^c Abundance determined from sticky trap abundance per plot.

^d Abundance determined from visual abundance per plot.

vae were only marginally more abundant in late compared with early oat kill plots in 2010 ($F = 3.15$; $df = 2,53$; $P = 0.05$; Table 4) and were not significantly different in 2011. Abundance of the cabbage looper (a pest that migrates to Michigan annually)

was marginally significant with 85% higher abundance in plots with the intermediate compared with early kill dates in 2010 ($t = 2.50$, $df = 19$, $P = 0.05$) and their abundance was not significantly different in 2011.

Table 7. Mean \pm SEM natural enemy abundance in experimental plots across fixed effect: herbicide intensity (low or high) in 2010 and 2011

	Insect abundance (mean \pm SEM) ^a		Source of variation		
	Low herbicide intensity plots	High herbicide intensity plots	Herbicide intensity		
			df ^b	F	P
2010 major natural enemies					
Spined soldier bug ^c	2.61 \pm 0.73a	0.88 \pm 0.34b	1,19	15.43	<0.01
<i>Coleomegilla maculata</i> ^c	1.28 \pm 0.15a	0.75 \pm 0.11b	1,15	15.77	<0.01
<i>Propylea quatuordecimpunctata</i> ^c	0.93 \pm 0.12a	0.33 \pm 0.07b	1,15	21.34	<0.01
<i>Harmonia axyridis</i> ^c	0.07 \pm 0.02	0.06 \pm 0.03	1,20	0.30	0.59
Lady beetle larvae ^d	0.59 \pm 0.15	0.48 \pm 0.13	1,15	0.84	0.37
Minute pirate bug ^c	6.44 \pm 0.75a	2.20 \pm 0.32b	1,19	23.49	<0.01
Predatory thrips ^c	13.98 \pm 1.37	18.39 \pm 2.16	1,15	0.02	0.88
<i>Cotesia rubecula</i> ^c	6.64 \pm 0.97	9.06 \pm 1.52	1,18	2.26	0.15
Chalcidoidea ^c	31.75 \pm 1.49a	28.17 \pm 1.63b	1,15	7.36	0.02
2011 major natural enemies					
Spined soldier bug ^c	0.50 \pm 0.26	0.65 \pm 0.24	1,19	0.65	0.43
<i>Coleomegilla maculata</i> ^c	1.25 \pm 0.14	1.07 \pm 0.12	1,15	0.16	0.70
<i>Propylea quatuordecimpunctata</i> ^c	0.13 \pm 0.03	0.14 \pm 0.04	1,15	0.11	0.75
Convergent lady beetle ^c	0.23 \pm 0.06	0.17 \pm 0.04	1,21	0.15	0.70
<i>Harmonia axyridis</i> ^c	0.02 \pm 0.02	0.04 \pm 0.02	1,15	0.89	0.36
Lady beetle larvae ^d	0.12 \pm 0.03	0.31 \pm 0.08	1,114	3.48	0.06
Minute pirate bug ^c	1.71 \pm 0.24a	0.93 \pm 0.12b	1,18	6.24	0.02
Predatory thrips ^c	3.22 \pm 0.34a	2.54 \pm 0.28b	1,15	9.95	<0.01
<i>Cotesia rubecula</i> ^c	1.47 \pm 0.26	1.41 \pm 0.25	1,19	0.97	0.33
<i>Diadegma insulare</i> ^c	2.83 \pm 0.64	3.12 \pm 0.69	1,15	0.13	0.72
Chalcidoidea ^c	23.72 \pm 1.70	23.29 \pm 1.97	1,19	0.04	0.84

^a Different letters indicate significant differences within row according to LSMeans ($\alpha = 0.05$).

^b Denominator degrees of freedom were calculated with the Kenward-Roger method (SAS 9.2, 2002–2008).

^c Abundance determined from sticky trap abundance per plot.

^d Abundance determined from visual abundance per plot.

Generalist predators such as lady beetle larva and adults responded positively to later oat kill dates (Table 6). In 2010, lady beetle larvae were three times more abundant where oats were killed later in the season compared with plots with oats killed at the intermediate date ($t = 2.58$, $df = 15$, $P = 0.05$). In 2011, lady beetle larvae were nearly five times more abundant in late kill date plots than in plots with early killed oats ($t = 3.45$, $df = 114$, $P < 0.01$).

In contrast with lady beetle larvae, greater abundance of lady beetle adults were only associated with later oat kill dates in 2011. Abundance of both *Propylaea quatuordecimpunctata* and convergent lady beetle adults were different among plots with different oat kill dates. *Propylaea quatuordecimpunctata* were three times more abundant in late than early kill date plots ($t = 2.56$, $df = 15$, $P = 0.03$). Convergent lady beetles were 77% more abundant in intermediate than late kill date plots ($t = 2.75$, $df = 21$, $P = 0.02$). However, abundance of another predator, predatory thrips, was not significantly different among treatments in 2010, and was only marginally significantly different in 2011, with 23% more in late compared with early oat kill date plots ($t = 2.58$, $df = 15$, $P = 0.05$).

Abundance of one species of parasitic wasp and one hyperparasitoid species responded to oat kill date (Table 6). The ichneumonid wasp, *Diadegma insulare*, a parasitoid that attacks the diamondback moth, was nearly twice as abundant in early kill date plots compared with plots where oats were killed later in the 2011 season ($t = 2.61$, $df = 15$, $P = 0.03$). A group of hyperparasitoids in the superfamily Chalcidoidea was 59% ($t = 6.92$, $df = 15$, $P < 0.01$) and 84% ($t = 2.51$, $df = 19$, $P = 0.04$) more abundant in plots with oats killed later in the season than plots with an early kill date, in 2010 and 2011, respectively.

Impact of Herbicide Intensity on Insect Abundance. Insect abundance was influenced by herbicide intensity but this varied by year for some species. Cabbage loopers were 40% more abundant in high herbicide intensity plots compared with low herbicide intensity plots ($t = 2.34$, $df = 19$, $P = 0.03$), although cabbage looper abundance was not affected by our treatments in 2011. In 2010 cabbage aphids were nearly three times more abundant in high compared with low herbicide intensity plots ($t = 7.81$, $df = 14$, $P < 0.01$). In 2011, this trend remained the same, but aphids were only 28% more abundant ($t = 3.15$, $df = 15$, $P < 0.01$). In 2011, 20% more imported cabbage-worm larvae were found in high ($t = 2.32$, $df = 15$, $P = 0.04$; Table 5) compared with low herbicide intensity plots.

Generalist predators, including *Podisus maculiventris*, *Coleomegilla maculata*, *Propylaea quatuordecimpunctata*, minute pirate bug, and predatory thrips were impacted by herbicide intensity in at least 1 yr (Table 7). *Podisus maculiventris* in 2010 were three times more abundant in low than in high herbicide intensity plots ($t = 3.93$, $df = 19$, $P < 0.01$) and in 2011, their abundance was not different across treatments. Although abundance of *C. maculata* in 2011 was not different, this lady beetle species was 70% more abun-

dant in low than high herbicide intensity plots in 2010 ($t = 3.97$, $df = 15$, $P < 0.01$). Another species, *Propylaea quatuordecimpunctata*, was three times more abundant in low compared with high herbicide intensity plots in 2010 ($t = 4.62$, $df = 15$, $P < 0.01$). The minute pirate bug was three times more abundant in low than high herbicide intensity plots in 2010 ($t = 4.85$, $df = 19$, $P < 0.01$) and 84% more abundant in low than high herbicide intensity plots in 2011 ($t = 2.04$, $df = 18$, $P = 0.04$). In 2011, predatory thrips were 27% more abundant in low compared with high herbicide intensity plots ($t = 3.15$, $df = 15$, $P < 0.01$).

Although abundance of parasitic wasps at the third trophic level did not differ across herbicide intensity treatments, a member of the fourth trophic level, in the superfamily Chalcidoidea, was 13% more abundant in low compared with high herbicide intensity plots in 2010 ($t = 2.71$, $df = 19$, $P = 0.02$; Table 7).

Insect Functional Groups. The effect of habitat complexity on functional groups in cabbage was examined using Hedge's D effect size. Any significant heterogeneity indicates significant differences between our two extreme treatments (e.g., low herbicide intensity with oats killed late and high herbicide intensity with oats killed early). Positive or negative effect sizes indicate a positive or negative impact of habitat complexity. We detected significant heterogeneity of effect sizes in 2010 ($Q_T > 232.28$, $P < 0.01$; $n > 180$) and in 2011 ($Q_T > 247.36$, $P < 0.01$; $n > 184$) for herbivore abundance, and natural enemy abundance. Life stages of insects did not explain heterogeneity in effect sizes in 2010 ($Q_B = 5.26$, $P = 0.20$) or 2011 ($Q_B = 3.64$, $P = 0.30$), (data not shown). Location of insects in the field also did not explain variation in effect sizes in 2010 ($Q_B = 0.39$, $P = 0.82$) or 2011 ($Q_B = 1.14$, $P = 0.57$), (data not shown). However, effect sizes between functional feeding groups was significant in 2011 ($Q_B = 9.73$, $P = 0.02$), although this category was not significant in 2010 ($Q_B = 1.37$, $P = 0.50$; Fig. 2). Predators were more abundant in high habitat complexity plots with a small effect size. There was no effect of habitat complexity on herbivores or parasitoids. Effect sizes were not significant between herbivores with different feeding guilds in 2010 ($Q_B = 0.46$, $P = 0.79$); however, feeding guild did account for effect size variation in 2011 ($Q_B = 10.63$, $P < 0.01$) when chewing herbivores and nonfeeding insects were less abundant in high complexity plots. Effect sizes for chewing and nonfeeding insects were small in 2011. Effect sizes between groups with different diet breadths were significant in 2010 ($Q_B = 8.59$, $P = 0.01$) and in 2011 ($Q_B = 6.09$, $P = 0.05$). Oligophagous herbivores were less abundant in high complexity plots in 2010 with a moderate effect size, and in 2011, specialist feeders were reduced in high complexity plots. Habitat complexity led to a small effect size for specialist feeders. Effect sizes between groups of natural enemies with different hunting modes (e.g., active or sit and wait) were significant in 2011 ($Q_B = 13.84$, $P < 0.01$), although not in 2010 ($Q_B = 2.25$, $P = 0.52$). In 2011, a small and moderate effect size was observed for active and for sit and wait predator abun-

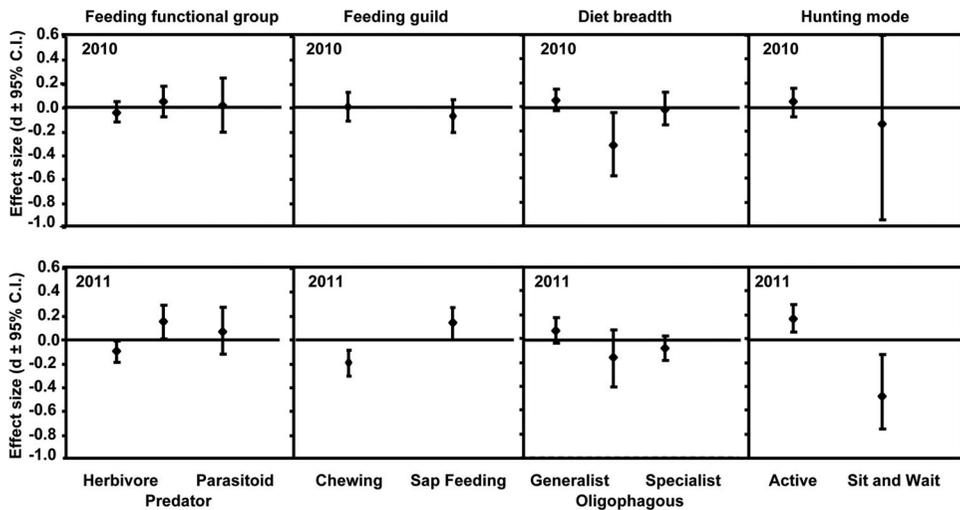


Fig. 2. Effect of habitat complexity on insect abundance classified according to functional feeding groups, feeding guilds, diet breadth, and hunting modes. Error bars indicate 95% bootstrap confidence intervals. Graphs in the top row are data from 2010, and in the bottom row are from 2011.

dance, respectively. Active hunters were more abundant in high complexity plots, whereas sit and wait predators were more prevalent in low complexity plots.

Discussion

This study examined the impact of vegetational and structural complexity, created by the presence of weeds and oat mulch in cabbage fields, on arthropod communities. We investigated how habitat complexity between cabbage rows affected natural enemy and pest community structure, individual insect species abundance, and insect guilds based on functional traits.

Insect Community Structure. Changes in habitat complexity influenced community structure of both herbivore and natural enemies in cabbage. In 2010, herbivore communities were influenced strongly by herbicide intensity (Fig. 1A), which affected the abundance of weeds (Table 2). In 2011, when weed pressure was lower, herbivore communities were influenced primarily by oat kill date (Fig. 1A), which determined the amount of oat mulch between cabbage rows (Table 2). This separation of herbivore communities along low and high complexity treatments regardless of how complexity was achieved indicates that multiple methods of habitat management can be used to shape herbivore community structure in this system. Natural enemy communities in both years were more influenced by oat kill date than by herbicide intensity (Fig. 1B), which may be the result of natural enemy communities dominated by species that are more responsive to indirect resources such as refuge. In general, our results support the idea that most herbivores (Risch et al. 1983) and natural enemies (Langellotto and Denno 2004) are responsive to changes in habitat complexity in agroecosystems.

Insect Abundance. Diversified agroecosystems are expected to harbor fewer pests (Risch et al. 1983), but

there can be significant deviations from this based on pest species and year. Contrary to past studies in crucifer crops and onions, several herbivore species and natural enemies did not respond to changes in habitat complexity, including the diamondback moth, onion thrips, *Phyllotreta cruciferae*, *Harmonia axyridis*, and the parasitoid, *Cotesia rubecula* (Zhao et al. 1992, Schellhorn and Sork 1997, Harvey and Eubanks 2004, Larentzaki et al. 2008, Alhmedi et al. 2009).

Impact of Oat Kill Date on Insect Abundance. Increasing habitat complexity with oat mulch had marginally positive effects on the specialist imported cabbageworm; however, a past study with rye mulch found reduced imported cabbageworm populations (Bottenberg et al. 1997).

In 2011, predators such as convergent lady beetles, *Propylaea quatuordecimpunctata*, lady beetle larvae, and predatory thrips responded positively to the presence of oat mulch in between rows. Although several of these species have responded similarly to mulching in other crops, such as potato (*Solanum tuberosum* L.) and sweet corn (Brust 1994, Lundgren et al. 2009), our results for predatory thrips and lady beetles, are contrary to results from mulched versus nonmulched onion plots (Larentzaki et al. 2008) and a meta-analysis conducted by Langellotto and Denno (2004).

Contrary to the generalist predators in our cabbage fields, a specialized natural enemy (*Diadegma insulare*) was impacted negatively by the two later oat kill dates, with reduced abundance in 2011. Habitat complexity created by noncrop flowering plants can increase *D. insulare* parasitism and abundance (Lee and Heimpel 2005), but the weeds in our experimental plots, that may have provided this type of resource, were apparently not able to exert a positive effect on this species because herbicide intensity was not significant. Other *Diadegma* spp. that attack diamondback moth larvae rely on chemical cues from host

plants (Rossbach et al. 2005) and visual cues to find its host (Wang and Keller 2002), and the greater oat mulch in between cabbage rows provided by later oat kill dates may have interfered with these cues, reducing oviposition or survival of *D. insulare* in our complex habitats. The superfamily Chalcidoidea consisting of hyperparasitoids of *D. insulare* and *C. rubecula*, were more abundant in the plots with later oat kill dates in 2010 and 2011, and lower herbicide intensity in 2010. Although habitat complexity in cabbage, including flowering borders had mixed results on hyperparasitism (Lee and Heimpel 2005, Jonsson 2009), these hyperparasitoids may be responsible for reduced parasitoid abundance in complex habitats in our cabbage field.

Impact of Herbicide Intensity on Insect Abundance. Increasing vegetational complexity had positive effects on the specialist imported cabbageworm in past studies (Latheef and Ortiz 1983, Maguire 1984). However, for several of our key herbivore species, our findings of a negative relationship between imported cabbageworm, cabbage aphid, and cabbage looper abundance and herbicide intensity, supports previous results from broccoli, cauliflower, and collards with vegetational complexity (Altieri et al. 1985, Altieri and Schmidt 1987, Garcia and Altieri 1992, Schellhorn and Sork 1997, Norris and Kogan 2000, Hooks and Johnson 2002). In these cases, complex row middles because of reduced herbicide intensity may reduce the encounter rate with the host plant and eventually reduce the amount of time spent on cabbage (Finch and Collier 2000). If weed species are preferred over an adjacent crop, the weeds may act as a barrier or a trap crop (Andow 1988).

Predators were generally positively impacted by vegetational complexity in between cabbage rows. Predator species, including *Podisus maculiventris*, minute pirate bug, *Coleomegilla maculata*, and *Propylaea quatuordecimpunctata* were more abundant in plots with greater weed pressure in 2010.

Although the exact mechanisms for our results, including positive responses to habitat complexity, are yet unknown, they support suggestions that natural enemies may find shelter, additional resources, or alternative prey within these complex habitats (Root 1973, Landis et al. 2000, Sunderland and Samu 2000). The enemies hypothesis (Elton 1958) suggests that increased habitat complexity will increase attack rates of herbivores by natural enemies; however, in other studies in cabbage, reduced predation and parasitism have been observed in intercropped plots and higher biocontrol in monocultures (Bjorkman et al. 2010, Adati et al. 2011). Complex habitats with noncrop plants such as weeds can host a greater diversity of herbivores, supporting a greater diversity of natural enemies within an agricultural field (Andow 1988). In our cabbage field, the weeds and oat mulch in between cabbage rows may be habitat for alternative prey.

Insect Functional Groups. Research in other agricultural systems (e.g., wheat, canola, cover crops, and corn) and in natural habitats often have focused on the relationship between habitat complexity and individual arthropod species or a single group of arthropods,

such as ground beetles (Carmona and Landis 1999, de la Pena et al. 2003, Harvey et al. 2008, Hummel et al. 2012). The use of functional traits is suggested to provide a view of communities, although providing information beyond the species level (McGill et al. 2006). Categorical classification can also provide an understanding of how treatments influence insect groups, particularly when every insect cannot be classified to species (Buschke and Seaman 2011). Studies that examined the influence of vegetational complexity on natural enemy communities in agroecosystems or natural habitats, have determined that vegetational complexity affects insect community structure across multiple trophic levels or functional groups (Tylianakis et al. 2007, Haddad et al. 2011). In this study, we found that predators were positively impacted in our high complexity plots in 2011, according to a significant positive effect size. This appears to support the positive responses of predator abundance to our habitat complexity treatments and previous findings of greater predator abundance in cabbage plots with mulch (Xu et al. 2011) or weed communities (Schellhorn and Sork 1997). However, we found that the impact of habitat complexity treatments did not significantly differ among insect life stages or their location in the field; thus, these traits have low priority when ranking them for responsiveness to habitat complexity manipulation (McGill et al. 2006). Higher priority functional traits included feeding guild, diet breadth, and hunting mode. In 2011, our high habitat complexity treatments negatively affected chewing insects, as well as oligophagous and specialized feeders, suggesting that generalist herbivores benefited the most from habitat manipulation. This trend also has been found in natural habitats, including grasslands, with greater specialist herbivore richness within heavily grazed grasslands with low structural complexity and greater generalist herbivore abundance in heterogeneous environments at the landscape level (Batory et al. 2007). In 2011, active hunters were influenced positively by increased habitat complexity and sit-and-wait hunters were impacted negatively. This does not appear to support past observations, in which weeds and mulch increased the presence of both ground dwelling and web building spiders (Altieri et al. 1985, Riechert and Bishop 1990, Hooks and Johnson 2004, Langellotto and Denno 2004). As supported by the large number of web building spiders located on the oats in our field, and the species' known preference for structural complexity (Rypstra et al. 1999), this particular negative response of sit and wait hunters may be the result of our restricted sampling method on cabbage, rather than true reductions in hunter abundance. Behavioral traits, including functional feeding group, feeding guild, diet breadth, and hunting mode appear to be responsive traits to habitat management and should be considered in future studies.

Summary. As indicated by significant differences in weed biomass, oat height, and oat biomass across our treatments, our cabbage field contained habitats with varying degrees of complexity between rows. Our findings suggest that greater habitat complexity be-

tween cabbage rows can reduce some pests, although enhancing predator populations. However, this complexity reduced cabbage yield, increased populations of other pests, and enhanced hyperparasitoid abundance, which may reduce the efficiency of the natural enemies in providing effective biological control within the field. We cannot eliminate the possibility that cabbage yield and quality may also play a role in the responses of individual species. Cabbage biomass and yields, midseason and at-harvest respectively, were reduced because of interactions between cabbage, weeds, and oats in 2010. Other studies also have observed cabbage yield reductions in killed oat plots (Bottenberg et al. 1997, Mochizuki et al. 2008). Further studies are needed to determine management strategies that improve arthropod management although minimizing weed and cover crop interference with the crop. It would also be helpful to determine the exact mechanisms responsible for the observed arthropod responses across mulching and weed pressure gradients.

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