

**INFLUENCE OF LIVING AND NON-LIVING HABITAT COMPLEXITY ON
ARTHROPODS IN STRIP-TILLED CABBAGE FIELDS**

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ABSTRACT

INFLUENCE OF LIVING AND NON-LIVING HABITAT COMPLEXITY ON ARTHROPODS IN STRIP-TILLED CABBAGE FIELDS

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Vegetational (living) and structural (non-living) complexity can influence arthropods in agricultural systems. In this thesis, both forms of complexity were manipulated in cabbage fields. In 2010 and 2011, a field experiment was conducted examining the effects of herbicide intensity and oat kill date on arthropods, weeds, and crop yield. Reduced herbicide intensity was associated with 1) lower abundance of several key cabbage pests and, 2) greater abundance of important natural enemy species. Habitats with both later oat kill dates or 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. In 2012, mulch species and mulch management practices were examined. Although mulching did not provide significant pest suppression, several generalist and one specialist parasitoid responded positively to habitat complexity. Predation and parasitism rates determined from natural enemy exclusion cages indicated no impact of mulching on the biocontrol of a major cabbage pest, the imported cabbageworm. In 2012, natural enemy behavior was observed in a y-tube olfactometer to determine the role of odor cues from decaying mulch on habitat choice. In general, natural enemies were not attracted or repelled by mulch odors. Further work is needed before implementation of these habitat management strategies (e.g. mulching and reduced weed management) and caution should be taken to avoid reducing cabbage yields or enhancing hyperparasitism.

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CHAPTER 1.

Habitat complexity and managing arthropods in cabbage

Introduction. Plants in the family Brassicaceae are considered one of the oldest groups of cultivated plants in the world, with archaeological evidence of human use dating back to 5000 BC (Ahuja et al. 2011). Even today, these plants are playing an important role in global agriculture. In 2010, global production of *Brassica sp.* exceeded 2.25 million hectares and yielded over 66.4 million tons (FAO, 2010). This family contains a variety of plants considered crops, ornamentals, and weeds with uses ranging from food for humans and livestock to oil, medicines, and renewable bio-energy. Among the *Brassica* crops commonly harvested, global production of cabbage (*Brassica oleracea*) is greater than any other *Brassica* crop grown for human consumption (Ahuja et al. 2011).

The United States has consistently been ranked in the top six countries in cabbage production (USDA-NASS, 2011). In 2011, 66,900 acres of cabbage were planted in the United States for the fresh market. Total production of cabbage in 2011 was greater than 21 million cwt, valued at \$368,311,000 (USDA-NASS, 2011).

Michigan has a long history of vegetable production, with a great diversity of fresh market vegetables, including *Brassica* crops. In the United States, Michigan is ranked 10th in fresh market cabbage production with 759 thousand cwt of fresh market cabbage produced in 2011 (NASS). With the majority of Michigan cabbage being grown for fresh market, threats from diseases, weeds, and insects pose severe challenges to achieving marketable cabbage heads. Weather conditions and the loam soils in southern Michigan are ideal for cabbage production.

Insect pests in cabbage. Marketability of cabbage heads declines when insect feeding reduces biomass, contaminates the harvestable parts with frass, and causes cosmetic damage. The diversity of insect pest species attacking Michigan cabbages poses a challenge to maintain quality with economical and sustainable tools. Insects such as the diamondback moth (*Plutella xylostella*, Lepidoptera: Plutellidae), imported cabbageworm (*Pieris rapae*, Lepidoptera: Pieridae), cabbage looper (*Trichoplusia ni*, Lepidoptera: Noctuidae), crucifer flea beetle (*Phyllotreta cruciferae*, Coleoptera: Chrysomelidae), and striped flea beetle (*Phyllotreta striolata*, Coleoptera: Chrysomelidae) chew characteristic holes, damaging cabbage leaves and heads (Figure 1.1). Other insects, such as cabbage aphids (*Brevicoryne brassicae*, Hemiptera: Aphididae), green peach aphids (*Myzus persicae*, Hemiptera: Aphididae), onion thrips (*Thrips tabaci*, Thysanoptera: Thripidae), and white flies (Hemiptera: Aleyrodidae), pierce cabbage tissue and remove plant sap (Figure 1.1). This feeding can reduce plant growth, cause characteristic leaf chlorosis and leaf curling, and introduce or facilitate plant diseases such as molds (Leite et al. 2006). In addition to reducing marketable yield, damage from insect pests can lead to 90% crop losses in severe cases (Ahuja et al. 2011). Management strategies to prevent yield and crop losses often focus on individual pests or a complex of pests. In cabbage, lepidopteran pests (e.g. diamondback moth, imported cabbageworm, and cabbage looper) cause the greatest damage in Michigan cabbage and management strategies often focus on these pests. The current global expense for managing one of these lepidopteran pests, the diamondback moth (*Plutella xylostella*, Lepidoptera: Plutellidae), and crop losses due to this pest, exceeds a billion dollars a year (Grzywacz et al 2010).

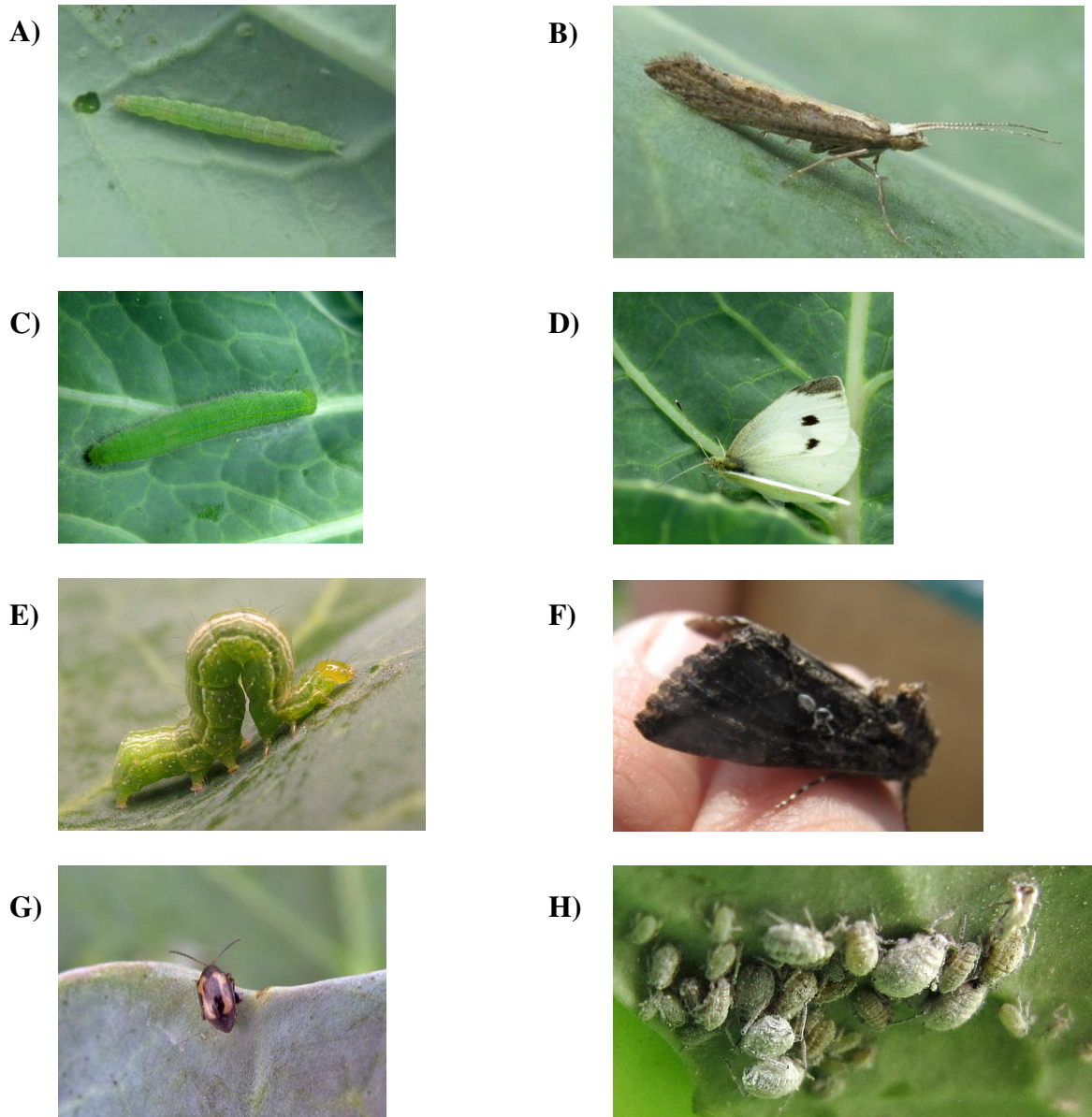


Figure 1.1. Major pests in Michigan cabbage. Top row: diamondback moth (*Plutella xylostella*, Lepidoptera: Plutellidae) larva (A) and adult (B), Second row: imported cabbageworm (*Pieris rapae*, Lepidoptera: Pieridae) larva (C) and adult (D), Third row: cabbage looper (*Trichoplusia ni*, Lepidoptera: Noctuidae) larva (E) and adult (F), Bottom row: striped flea beetle (*Phyllotreta striolata*, Coleoptera: Chrysomelidae) (G) and cabbage aphids (*Brevicoryne brassicae*, Hemiptera: Aphididae) (H). For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

Chemical control in cabbage fields. Traditionally, conventional management practices for insect pests in cabbage include pesticide applications according to calendar dates without considering thresholds (Hutchison and Burkness 1999). In addition to costs associated with this overuse of insecticides, current chemical controls have led to development of insecticide resistance to major insecticides commonly included in cabbage spray schedules (e.g. pyrethroids and carbamates) (Leibee and Savage 1992). In the United States, insecticide resistance has been observed in major cabbage pests, such as the cabbage looper and diamondback moth, creating challenges for growers relying primarily on chemical controls (Wilkinson et al. 1983, Leibee and Savage 1992). Even *Bt* sprays that are often considered better alternatives to synthetic insecticides due to their high specificity and limited environmental impacts, have led to insecticide resistance. This phenomenon has been observed in diamondback moth and cabbage looper populations (Talekar and Shelton 1993, Janmaat and Myers 2003).

Chemical controls have negative impacts on the ecosystem because agricultural fields are open systems, connected to the surrounding landscape. Chemical inputs such as fertilizer and pesticides do not remain in the field. Run off and drift from pesticide applications can cause mortality of terrestrial and aquatic organisms in adjacent ecosystems (e.g. Burn 2003), as well as chronic impacts on surrounding wildlife (e.g. Poletta et al. 2009). Negative impacts of pesticide use can also be observed within the agroecosystem itself. In particular, non-target organisms that would otherwise provide free pest management and pollination services can be negatively impacted (Haseeb and Amano 2002, Desneux et al. 2007, Pekar and Benes 2008, Johnson et al. 2010).

Concerns over insecticide resistance and environmental impacts of widespread pesticide use have led scientists to look for alternative management strategies for cabbage pests and many

growers are turning to Integrative Pest Management (IPM) strategies. IPM emphasizes the use of pest monitoring, appropriate pest thresholds, selective insecticides, and insecticide rotation to reduce development of resistance. IPM strategies also incorporate other modes of pest management, including biological control.

Natural biological control in cabbage fields. Although there is a diverse community of insect pests attacking Michigan cabbage, there is also a diverse community of natural enemies providing natural biological control in these fields. Common predators include lady beetles (Coleoptera: Coccinellidae), ground beetles (Coleoptera: Carabidae), predatory thrips (Thysanoptera: Aeolothripidae), damsel bugs (Hemiptera: Nabidae), big-eyed bugs (Hemiptera: Geocoridae), spiders (Araneae), and harvestman (Opiliones) (Figure 1.2). Parasitoids also provide pest suppression, including tachinid flies (Diptera: Tachinidae) and specialists such as *Diadegma insulare* (Hymenoptera: Ichneumonidae) and *Cotesia rubecula* (Hymenoptera: Braconidae) that attack the diamondback moth and imported cabbageworm respectively (Figure 1.2).

Natural enemies can provide substantial biological control in cabbage fields. Studies have found significant mortality of the imported cabbageworm in cabbage fields, with predation rates up to 80% (Schmaedick and Shelton 1999). Long term studies in Minnesota have observed parasitism rates of this pest as high as 50% (Wold-Burkness et al. 2005). These ecosystem services are provided by arthropods naturally found in the field. However, insecticide applications can reduce natural enemy abundance, predation, and parasitism in cabbage fields (Bommarco et al. 2011), often leading to greater pest populations and investment in pest management by growers. Secondary pest outbreaks also result from the loss of natural enemies.

Although usually considered a minor threat to vegetable crops, without the natural enemies that usually suppress their populations, secondary pests can cause severe damage and crop loss.

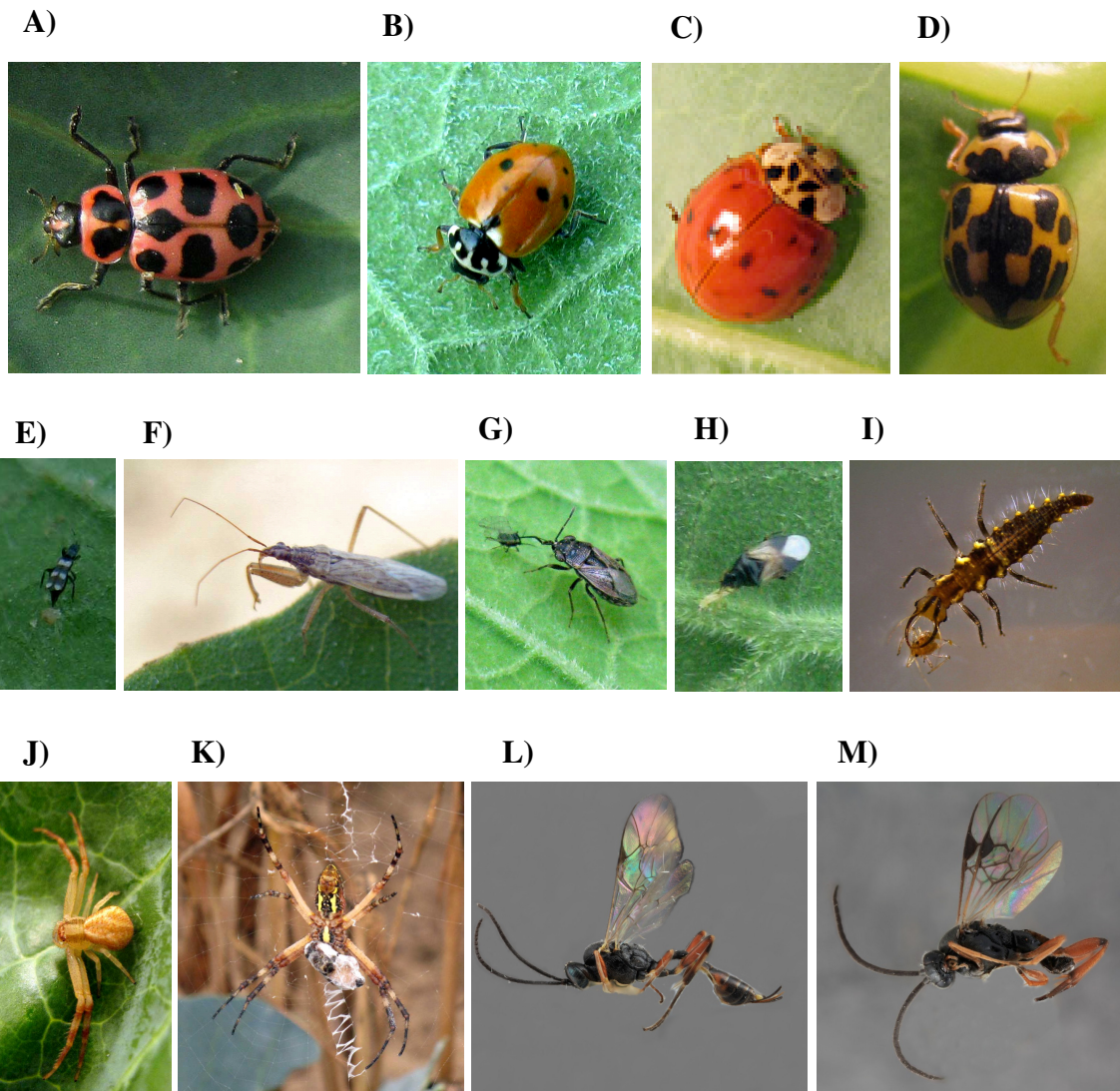


Figure 1.2. Common natural enemies in Michigan cabbage. Top row: lady beetles (Coleoptera: Coccinellidae)(A-D), Second row: predatory thrips (Thysanoptera: Aeolothripidae)(E), damsel bugs (Hemiptera: Nabidae)(F), big-eyed bugs (Hemiptera: Geocoridae)(G), minute pirate bug (Hemiptera: Anthocoridae)(H), lacewing larva (Neuroptera: Chrysopidae)(I), Third row: spiders (Araneae)(J-K), *Diadegma insulare* (Hymenoptera: Ichneumonidae)(L) and *Cotesia rubecula* (Hymenoptera: Braconidae)(M).

Habitat complexity and conservation biological control. Natural enemy populations can be conserved by manipulating habitat. While conventional cabbage management practices may reduce natural enemy populations, my thesis aimed to examine alternative habitat management techniques that increase habitat complexity within a field and in turn, enhance biological control of cabbage pests. Past studies have primarily examined habitat management strategies such as vegetation borders, intercropping, and undersowing cabbage with living mulches to create habitat complexity.

Non-crop borders include the planting of vegetational strips along the borders of an agricultural field or the presence of natural vegetation adjacent to field margins. Much of this work has examined the impact of floral borders in reducing pest populations and enhancing natural enemy populations and biological control (Bigger and Chaney 1998, Lee and Heimpel 2005, Winkler et al. 2010), with particular attention to the relationship between floral resources and effects on parasitoids (Lee et al. 2006, Lee and Heimpel 2008).

Habitat management such as intercropping and undersowing includes the planting of a cash crop with a companion plant or a cover crop, increasing the complexity *within* the field. In cabbage, intercropping can reduce pest populations (Theunissen et al. 1995, Vidal 1997, Lynch and Zobel 2002, Hooks and Johnson 2003, Xu et al. 2010) and lead to greater natural enemy populations (Armstrong and McKinlay 1997). In this thesis I also examined alternative management strategies for creating habitat complexity *within* the field, such as reduced herbicide management, strip tillage, and cover crop mulching.

Structural and vegetational complexity in Michigan cabbage. Habitat complexity can be separated into non-living and living complexity (Rypstra et al. 1999, Finke and Denno 2002).

Based on these measurements, two components create habitat complexity. First, structural complexity includes plant architecture, size, and height of non-living structures such as mulch. Second, vegetational complexity includes properties of living vegetation, such as biomass and plant diversity (McNett and Rypstra 2000, Shrewsbury and Raupp 2000, Obermaier et al. 2008). In this thesis, I examined the effects of both structural complexity (e.g. amount of mulch in between cabbage rows) and vegetational complexity (e.g. amount of weed biomass in between cabbage rows) on arthropod communities.

Reducing herbicide intensity increases the weed biomass in between cabbage rows, therefore creating vegetational complexity in the field. In other *Brassica* crops, greater vegetational complexity due to weeds can reduce pest populations, although this is highly dependent on weed species (Schellhorn and Sork 1997). Combining strip tillage and killed cover crops creates structural complexity. Strip tillage is a form of reduced tillage in which planting rows are tilled, leaving soil undisturbed between rows. After killing a fall or spring planted cover crop, strip tilling of the field leaves cover crop mulch on the soil surface between planting rows. Benefits of allowing cover crop mulch to remain on the soil surface in cabbage fields have been observed, including maintaining soil moisture, reducing soil temperatures (Mochizuki et al. 2008), and providing weed suppression (Bottenberg et al. 1997).

Structural complexity can be further manipulated by choosing cover crops with different physical properties (e.g. leaf area, biomass) or manipulating the physical structure with further management techniques (e.g. rolling, crimping). Cover crop species such as legumes and cereals have different physical properties that have influenced cabbage yield, cabbage quality, weed suppression, and insect abundance (Morse and Seward 1986, Nelson et al. 1991, Mangan et al. 1995, Mwaja et al. 1996, Masiunas et al. 1997). Rolling and chopping these mulches have also

had a significant negative and neutral impact on cabbage yield respectively (Mochizuki et al. 2008).

Although the effects of weed biomass, the presence of mulch, and mulch management on weed suppression and cabbage yields have been examined, limited research has examined the impacts across multiple trophic levels especially as it pertains to biological control.

Mechanisms for response of natural enemies to habitat complexity. Theoretically, complex habitats should reduce pest populations directly by acting as a trap crop and interfering with the movement, landing, and oviposition of pests into the field or attracting the pest away from the cash crop (Andow 1988, Finch and Collier 2000, Broad et al. 2008). However, complex *Brassica* habitats may also provide additional resources for pests such as nectar and pollen, directly influencing arthropod abundance (Zhao et al. 1992).

According to the natural enemy hypothesis (Elton 1958), complex habitats can provide refuge, alternative prey, additional resources, and protection from intraguild predation, enhancing natural enemy populations or hunting efficiency directly (Root 1973, Landis et al. 2000, Sunderland and Samu 2000).

These complex habitats can also indirectly influence arthropod abundance. Complex habitats can support greater herbivore species richness, enhancing natural enemy populations (Andow 1988). These same habitats can also influence hunting behavior of predators, influencing predation and herbivore populations (Andow 1988). Additionally, natural enemies rely on visual and odor cues when choosing habitats and locating herbivores (Adedipe and Park 2010, Randkofer et al. 2011). Vegetation and structural complexity may reduce herbivore populations if cues from these habitats are attractive to natural enemies at higher trophic levels,

leading to greater biological control of herbivores (Kaplan 2012). Alternatively, habitat complexity may interfere with hunting and reduce efficiency of natural enemies through the interference of visual or odor cues, enhancing herbivore populations at lower trophic levels (Randkofer et al. 2011, Harvey and Fortuna 2012).

In summary, complex habitats may directly influence the abundance of an arthropod through changes in the environment or the arthropod's behavior (Figure 1.3) or indirectly influence arthropods through changes in abundance or efficiency of arthropods at higher or lower trophic levels (Figure 1.4).

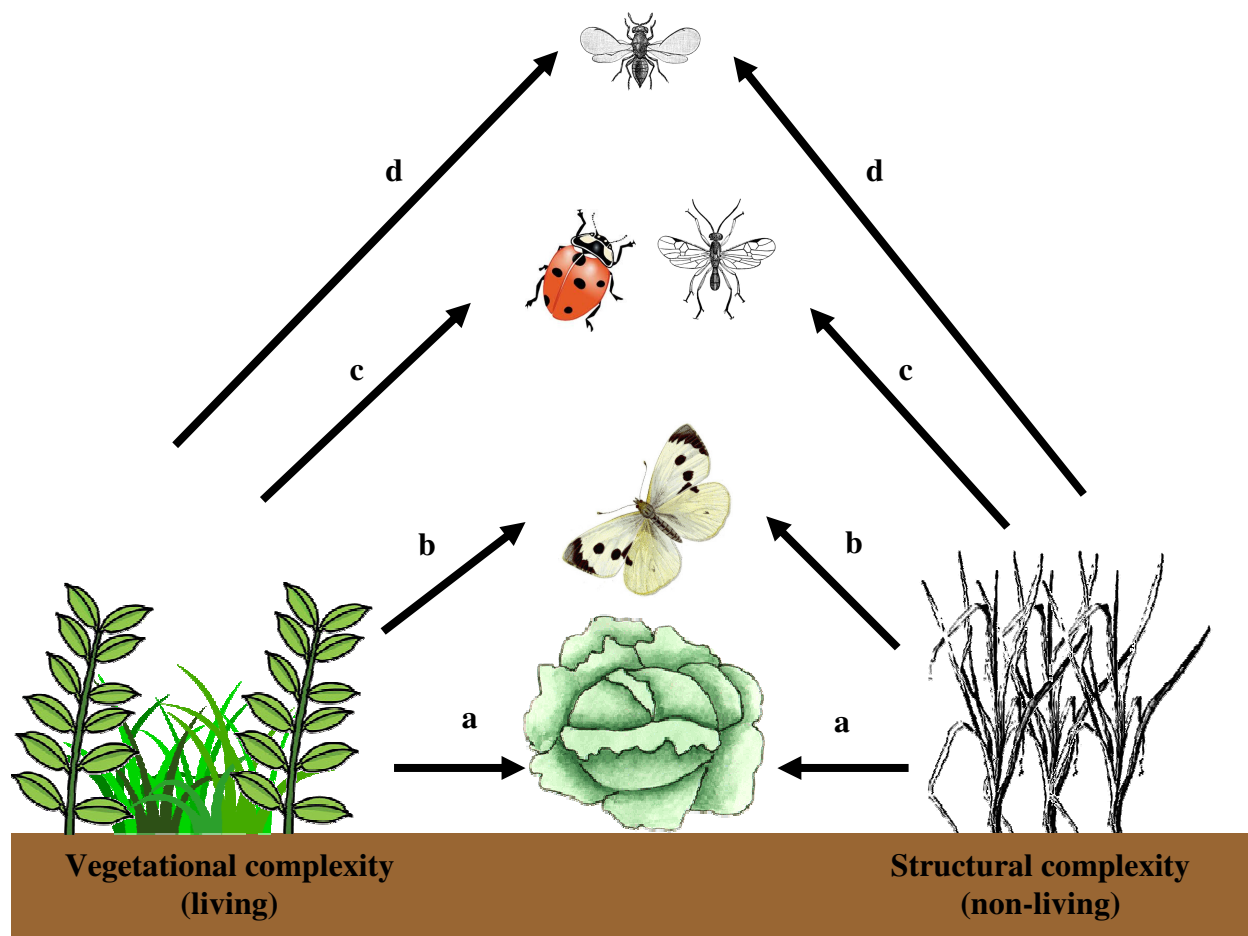


Figure 1.3. Direct impacts of habitat complexity on trophic levels in cabbage fields. Direct effects include a) Influencing cabbage yield and quality, b) Influencing pest abundance positively (e.g. provide shelter, protection, and resources or negatively (e.g. interferes with landing and movement of pest), c) Influencing natural enemy abundance positively (e.g. provide shelter, protection, and resources) or negatively (e.g. interferes with search efficiency or chemical and visual cues), and d) Influencing hyperparasitoid abundance positively (e.g. provide shelter, protection, and resources) or negatively (e.g. interferes with chemical or visual cues when searching for hosts)

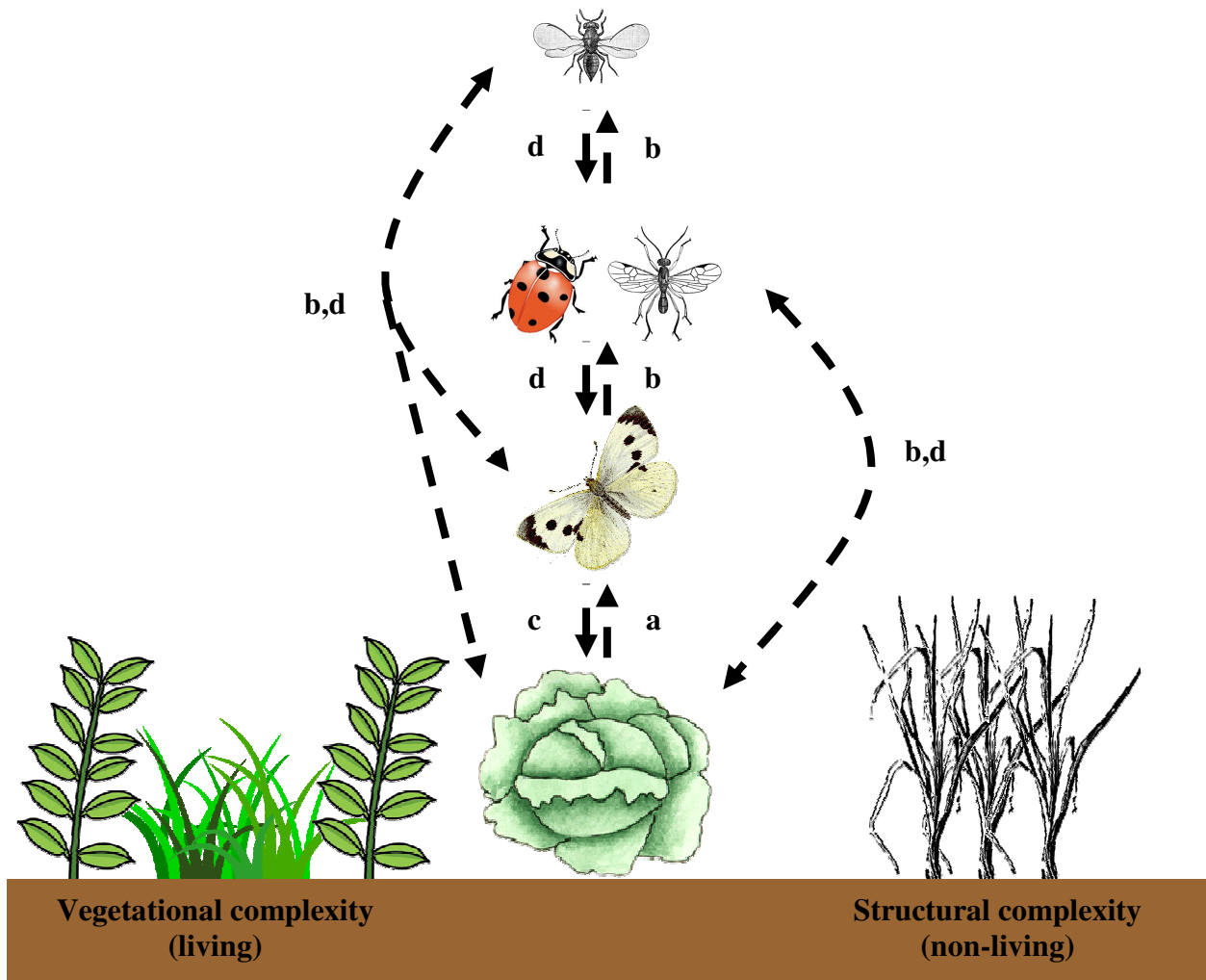


Figure 1.4. Indirect impacts of habitat complexity on trophic levels in cabbage fields. For instance, a) habitat complexity can change cabbage size and quality influencing pest populations, b) habitat complexity can change arthropod abundance and location in the field, influencing habitat choices of higher trophic levels. Changes at higher trophic levels influence lower trophic levels. For instance, c) habitat complexity affects pest abundance which can influence cabbage yield and quality or d) habitat complexity can change predator and parasitoid abundance or efficiency influencing predation and parasitism of lower trophic levels.

Thesis objectives. Ultimately the goal of this thesis was to examine alternative management strategies for pests such as the imported cabbageworm. The first two objectives of this thesis examined the impact of vegetational and structural habitat complexity on arthropods and biological control in Michigan cabbage fields. The first objective examined the impacts of habitat management strategies such as reduced herbicide intensity, strip tillage, and cover crop mulching on arthropod community structures and abundance. The second objective examined the impact of different mulch species and the height of the mulch on the arthropod community and biological control using a field-based technique. The final objective of this thesis was to begin to determine the mechanisms responsible for trends in natural enemy abundance observed in the field. In particular, the role of odor cues from mulch on the behavior of natural enemies was examined.

CHAPTER 2.

Cover crop mulch and weed management influence

arthropod communities in strip-tilled cabbage

Introduction. 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 non-living and living structural complexity (Rypstra et al. 1999, Finke and Denno 2002). This includes architecture and/or size of non-living structures (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 non-living 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 agroecosystems, habitats with high non-living 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 generalist predator in corn, was also reduced in polycultures compared to 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 using behavior-modifying tools such as habitat modification of agroecosystems is challenging because the goal is to enhance crop yields, while reducing pests and increasing 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, Tschamntke et al. (2008) demonstrated that although generalist natural enemy diversity was preserved in complex landscapes, specialized natural enemies were not, due to 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 pre-established cover crops (Nicholson and Wien 1983). Cover crops may act as dead mulches if killed prior to 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 while 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 while 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 (e.g. 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 (*e.g.* 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, due to 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 (*e.g.* Martin et al. 2001). For transplanted cabbage, CWFP studies (Weaver 1984) suggest that cover crops must be terminated within 3 to 4 weeks 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 pre-established 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 non-crop 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 (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 (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 are often 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, the crucifer flea beetle, *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 Hutchinson 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 sp.*, Hemiptera: Anthocoridae), and predatory thrips (*Aelothrips sp.*, Thysanoptera: Aeolothripidae). Lady beetle species are dominant predators, primarily the pink lady beetle (*Coleomegilla maculata* (DeGeer), Coleoptera: Coccinellidae), fourteen spotted lady beetle (*Propylaea quatuordecimpunctata* (Linnaeus), Coleoptera: Coccinellidae), multicolored Asian lady beetle (*Harmonia axyridis* (Pallas), Coleoptera Coccinellidae), and convergent lady beetle

(*Hippodamia convergens* (Guerin), Coleoptera: Coccinellidae).

Habitat management techniques, such as flowering strips (Pfiffner et al. 2009) and companion plants (Hooks and Johnson 2003) have been studied to enhance biological control of cabbage pests and enhance 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 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, while, 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. I performed a field study at Michigan State University's Horticulture Farm in East Lansing, Michigan. 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 six treatments and four replications. Treatments were a combination of two main effects: oat kill date (early, intermediate, or late) and herbicide intensity (low or high). Low herbicide intensity treatments received standard cabbage pre-emergence herbicides. High herbicide intensity treatments received pre-emergence herbicides and either an additional post-emergence herbicide (2010) or supplemental hand weeding (2011) to effectively exclude all weeds. In 2010, plots were 3.0 x 7.6 m, with 4 rows of cabbage spaced 76 cm apart. In 2011, plot size was increased to 4.6 x 9.1 m with 6 rows of cabbage per plot.

Field Operations. The dates of major field operations are provided in Table 2.1. In mid-April the entire experimental area was fertilized with 91 kg/ha of 19-19-19 (NPK), and oats (*Avena sativa* var. "Ida"; Zmitko Farm, Owosso, MI) were planted using a grain drill (Great Plains Compact Drill 3P606NT, Salina, Kansas). 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 (NPK) 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 (equipped with notched trash-cleaning discs, cutting-coulter, shank-point assembly, berming disks and rolling basket) was used to create 25 cm x 25 cm deep strips at 76 cm between-strip spacing. Pre-established oats were effectively killed in the strips, but minimally affected in the undisturbed 51 cm between strips, thus creating cover crop mulch between crop

rows. Following strip-tillage, a pre-transplant herbicide application containing Goal (0.28 kg active ingredient oxyfluorfen / ha) and Dual II Magnum (0.54 kg active ingredient s-metolachlor / ha) was applied in all treatments. For early oat kill-date treatments, Select 2EC (0.21 kg active ingredient clethodim / ha) was also applied at this time. Intermediate oat kill treatments with Select EC occurred 14 days 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 post-emergence herbicide application to manage broadleaf weeds 28 DAT (Goal, 0.28 kg active ingredient oxyfluorfen / ha); these plots were also hand-weeded 31 DAT. Due to reduced weed pressure in 2011, no additional post-emergence herbicides were applied in high herbicide intensity plots, though plots were hand-weeded at 29 and 71 DAT to remove escaped weeds.

Cabbage transplants (var. "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) prior to transplanting in the field. Cabbage was transplanted by hand on May 21, 2010 and May 31, 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.

Table 2.1. Dates of major field operations in 2010 and 2011.

Field operation	Date	
	2010	2011
Oats planted	14-Apr	14-Apr
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-Jun	9-Jun
Clethodim applied in late oat kill	17-Jun	21-Jun
Oxyflourfen applied in high herbicide intensity	11 June	NA
Urea sidedress application	22-Jun	27-Jun
Hand weeding	21-Jun	29-Jun
Hand weeding 2 in high herbicide intensity	NA	10-Aug
Cabbage harvest	17-Aug	8-Sep

Oat height and biomass. In 2010, I measured oat height in two 0.25 m² quadrats randomly placed in each plot. The heights of ten random oat plants per 0.25 m² quadrat were measured prior to 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 prior to weighing. In 2011, oat height was measured using the same methods as 2010. However, oat height was recorded 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 9 and 17 DAT, in intermediate and late kill-date plots respectively. Killed oat biomass was collected 0 and 3 d prior to oat kill-date in intermediate and late killed plots. 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 to 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 to 2010.

Cabbage biomass and yield. To determine mid-season cabbage plant biomass, I 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, Nebraska). 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 greater than 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 non-marketable), cabbage leaf area, and number of cabbage leaves per plant were assessed using a mixed model (PROC Mixed, SAS 9.2, 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 two years were analyzed separately.

Insect community assessment. Insects were sampled visually and with yellow sticky traps (7.5 × 12.3 cm, Great Lakes IPM, Vestaburg, MI) in the growing season for 9 wks in 2010 and 14 wks in 2011. Sessile insects were evaluated 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 treatments on insect community structure, cluster analysis (PROC Cluster) was used based on average abundance per treatment of each insect species. The analysis was repeated using average abundance per plot for each insect species. Herbivores and natural enemies were analyzed separately in both years. This type of cluster analysis uses average linkage distance to determine similarity between groups (Proc Cluster).

To determine the impact of treatments on individual species, a repeated measures analysis was used. Due to the difference in environmental conditions between 2010 and 2011 (e.g. precipitation, degree day accumulation), data from visual sampling and sticky traps was transformed using $\log(x + 0.01)$ and analyzed separately for 2010 and 2011. Analysis included 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). Covariates included marketable cabbage yield, total herbivore abundance, total predator abundance, total parasitoid abundance, and host abundance. For instance, diamondback moth abundance was included as a covariate for analyzing *Diadegma insulare* abundance and imported cabbageworm abundance was included as a covariate for *Cotesia rubecula* abundance. If main effects were significant ($\alpha=0.05$), we performed least-square means tests with Tukey-Kramer adjustment.

In order to identify how the herbicide intensity and oat kill date treatments influenced functional groups of natural enemies and herbivores, Hedge's *d* effect size (Cohen 1988) was calculated 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)(Supp. Table S1). Effect size was used to compare the effects of the two extreme treatments (high herbicide intensity and early oat kill date, compared to 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. A fixed effects model was used with categorical structure and included re-sampling 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, later oat kill date, weed management, and the interaction between these factors positively influenced oat height (Table 2.2). Within low and high herbicide intensity plots, oats were more than three times taller in late-killed oats, compared to 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 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 2.2). In 2010, late killed oats produced 173.63 g/ m^2 of biomass after termination, while early killed oat plots did not contain substantial oat biomass on sampling dates, since 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, herbicide intensity but not by oat kill date influenced weed biomass (Table 2.2). In 2010, low herbicide intensity plots produced 266 g/ m^2 biomass compared to only 2 g/ m^2 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 to 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. Oat kill date but not herbicide intensity influenced mid-season cabbage biomass and leaf area per plant in 2010 (Supp. 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 mid-season cabbage biomass

than late kill-date plots. While the leaf area per cabbage plant differed across oat kill date, the number of cabbage leaves per plant did not ($F = 0.84$, $df=2,15$, $P > 0.45$). In 2011, mid-season cabbage biomass, leaf area, and number of leaves did not differ across oat kill date or herbicide intensity ($F < 1.89$, $df=2,15$, $P > 0.19$; Supp. 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 to 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 2.2), due to a slightly earlier kill date relative to cabbage transplanting.

The final yield (Table 2.3) and number of marketable and non-marketable cabbage (Supp. Table S3) in 2010, was influenced by oat kill date. Marketable cabbage biomass was two times greater in early compared to 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 ($t = 2.10$, $df=15$, $P = 0.05$). Non-marketable heads were more abundant in late kill date plots compared to 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 to late kill date plots ($t = 3.24$, $df=15$, $P < 0.01$; Table 2.3). Herbicide intensity and oat kill date did not affect non-marketable yield. Non-marketable biomass and the number of marketable or non-marketable cabbage heads per plot in 2011 were not different across herbicide intensity ($F < 1.66$, $df=1,15$, $P > 0.21$; Table 2.3, Supp. 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 2.3, Supp. Table S3). In 2010, marketable cabbage weight

was reduced by 33% under low compared to high herbicide intensity treatments ($t = 3.04$, $P < 0.01$). Greater yield loss due to weeds in 2010 was likely the result of greater weed biomass in 2010 compared to 2011 (Table 2.2).

Insect community structure. In 2010, there were two distinct herbivore communities according to herbicide intensity (Fig. 2.1A). Herbivore communities were more similar between plots where oats were killed at an intermediate or later date compared to 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 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. 2.1B). 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.

Herbivore and natural enemy communities were examined across plots (Supplementary Figure S1). Although there was variation within treatments, plot clustering supports previous findings.

Insect abundance. Since interactions between main effects were not significant for insect abundance, only the results for main effects are presented. A couple herbivore and natural enemy species consistently did not respond to experimental treatments in 2010 or 2011. Abundance of the diamondback moth were not different among any of the oat kill date (Table 2.4) or herbicide intensity treatments (Table 2.5). In addition, the abundance of the ichneumonid wasp *Diadegma insulare*, a specialist parasitoid that attacks the diamondback moth, was not significantly different among treatments in either 2010 or 2011.

Impact of oat kill date on insect abundance. Oat kill date had an impact on herbivore abundance, for example the abundance of the cabbage looper (a pest that migrates to Michigan annually) tended to have 85% higher abundance in plots with the intermediate compared to early kill dates in 2010 ($t = 2.50$, $df=19$, $P = 0.05$). In 2011, abundance of the cabbage looper was more than 60% greater in early kill dates than intermediate or late kill dates ($t > 3.42$, $df= 28$, $P < 0.01$). Crucifer flea beetle abundance was 37% greater in late kill dates than earlier in the 2010 season ($t > 3.06$, $df= 26$, $P < 0.01$). Onion thrips abundance was 36% higher in intermediate compared to early kill date plots in 2011 ($t = 2.84$, $df= 27$, $P = 0.02$).

Generalist predators such as lady beetle larva and adults typically responded positively to later oat kill dates (Table 2.6). Lady beetle larvae were three times more abundant where oats were killed later in the season compared to plots with oats killed at the intermediate date in 2010 ($t = 2.58$, $df=15$, $P = 0.05$). Pink lady beetles were 99% more abundant in late than early kill date plots ($t = 3.07$, $df=20$, $P = 0.02$). Fourteen spotted lady beetles were three times more abundant in late than early kill date plots in 2011 ($t = 2.56$, $df=15$, $P = 0.03$) and predatory thrips were significantly different in 2011, with 25% more in intermediate compared to early oat kill date

plots ($t = 3.24$, $df=20$, $P = 0.01$). In contrast, convergent lady beetles were 77% more abundant in intermediate than late kill date plots in 2011 ($t = 2.89$, $df=24$, $P = 0.02$).

Abundance of one species of parasitic wasp and one hyperparasitoid species responded to oat kill date (Table 2.6). The braconid wasp, *Cotesia rubecula*, a parasitoid that attacks the imported cabbageworm, was 31% more abundant in late kill date plots compared to plots where oats were killed earlier in the 2011 season ($t = 12.72$, $df = 24$, $P = 0.03$). A group of hyperparasitoids in the superfamily Chalcidoidea was 59% ($t = 3.75$, $df=24$, $P < 0.01$) and 84% ($t = 4.03$, $df= 26$, $P < 0.01$) 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. In 2010, cabbage loopers were 40% more abundant in high herbicide intensity plots compared to low herbicide intensity plots in 2010 ($t = 2.34$, $df=19$, $P = 0.03$). In 2010, cabbage aphids were nearly three times more abundant in high compared with low herbicide intensity plots ($t = 8.31$, $df=23$, $P < 0.01$). 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 cabbageworm larvae were found in high ($t = 2.11$, $df = 24$, $P = 0.04$; Table 2.5) compared to low herbicide intensity plots.

Generalist predators, including the spined soldier bug, pink lady beetle, fourteen spotted lady beetle, and minute pirate bug were impacted by herbicide intensity in at least one year (Table 2.7). Spined soldier bugs in 2010 were three times more abundant in low than in high herbicide intensity plots ($t = 3.93$, $df = 19$, $P < 0.01$). Abundance of the pink lady beetle was 70% more abundant in low than high herbicide intensity plots in 2010 ($t = 4.26$, $df=24$, $P < 0.01$).

Another species, the fourteen spotted lady beetle, was three times more abundant in low compared to 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 ($t = 2.04$, $df=18$, $P = 0.04$).

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 ($t = 2.36$, $df= 24$, $P = 0.03$; Table 2.7).

Significant covariates for herbivores. Marketable cabbage yield was a significant covariate for cabbage aphids and crucifer flea beetles in 2010 ($F > 5.46$, $P < 0.02$) and imported cabbageworm in 2011 ($F = 10.21$, $df= 1,24$; $P = 0.01$). In these cases, greater marketable yield positively impacted cabbage aphid abundance and negatively impacted flea beetle and imported cabbageworm abundance. Total predator abundance was a significant covariate for the imported cabbageworm and diamondback moth in 2010 ($F > 4.43$, $P < 0.04$) and both cabbage loopers and onion thrips in 2011 ($F > 20.54$, $P < 0.01$). Predator abundance negatively impacted herbivore abundance, excluding onion thrips which were more abundant in plots with greater predator abundance.

Significant covariates for natural enemies. Marketable cabbage yield was a significant covariate for the pink lady beetle in both 2010 and 2011 ($F > 8.10$, $P < 0.01$), with fewer lady beetles in plots with greater marketable yield. Total herbivore abundance also affected pink lady

beetle abundance in 2011 ($F = 6.84$, $df = 1,252$; $P < 0.01$), with fewer herbivores in plots with the greatest number of pink lady beetles. Total predator abundance was a significant covariate for the pink lady beetle, fourteen spotted lady beetle, convergent lady beetle, lady beetle larvae, predatory thrips, *Cotesia rubecula*, *Diadegma insulare*, and Chalcidoidea hyperparasitoids ($F > 9.56$, $P < 0.02$). In general, greater abundance of these natural enemy species was found in plots with greater total predator abundance. Finally, abundance of the imported cabbageworm and *Cotesia rubecula* were significant covariates in at least one year for *C. rubecula* and its hyperparasitoids in the superfamily Chalcidoidea respectively ($F > 3.87$, $P < 0.05$), with host abundance positively influencing parasitoid or hyperparasitoid abundance.

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 the 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 and location of insects in the field 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). However, effect sizes between functional feeding groups was significant in 2011 ($Q_B = 9.73$, $P = 0.02$). Predators were more abundant in high habitat complexity plots with a significant, small effect size. There was no effect of habitat complexity on herbivores or parasitoids. Feeding guild did account for effect size variation in

2011 ($Q_B = 10.63$, $P < 0.01$) when chewing herbivores were less abundant in high complexity plots. Significant effect sizes for chewing and non-feeding insects were small in 2011. Effect sizes for 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 significant, moderate effect size. In 2011, specialist feeders were reduced in high complexity plots. Habitat complexity led to a significant, small effect size for specialist feeders. Effect sizes for 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 abundance, respectively. Active hunters were significantly more abundant in high complexity plots, whereas sit and wait predators were more prevalent in low complexity plots.

Table 2.2. Mean \pm SEM oat height, oat biomass, and weed biomass in 2010 and 2011.

Main effects	Oat height (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 \pm 0.0a	0.0 \pm 0.0a	0.0 \pm 0.0a	0.0 \pm 0.0a	167.28 \pm 83.09	9.03 \pm 5.92
Intermediate	8.21 \pm 0.51b	41.67 \pm 0.93b	NA	28.21 \pm 5.66b	131.21 \pm 51.96	34.15 \pm 15.79
Late	26.75 \pm 0.72c	46.56 \pm 1.53c	173.63 \pm 13.61b	87.06 \pm 8.40c	104.23 \pm 46.68	10.39 \pm 8.47
Herbicide intensity						
Low	11.11 \pm 3.17a	29.58 \pm 6.36	53.67 \pm 23.51	39.59 \pm 12.25	266.26 \pm 44.16a	35.71 \pm 10.83a
High	12.19 \pm 3.60b	29.24 \pm 6.34	62.08 \pm 27.22	37.26 \pm 11.51	2.22 \pm 1.08b	0.0 \pm 0.0b
Significance	-----P-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 x 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 LSMeans ($\alpha=0.05$).

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

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

Table 2.3. Mean \pm SEM non-marketable and marketable fresh weight of cabbage heads in 2010 and 2011.

Main effects	Marketable (kg) ^a		Non-marketable (kg) ^a	
	2010	2011	2010	2011
Oat kill date				
Early	48.51 \pm 3.54a	60.31 \pm 6.37a	0.36 \pm 0.14a	2.37 \pm 0.69
Intermediate	40.86 \pm 4.20a	50.20 \pm 7.28ab	1.83 \pm 0.77ab	3.56 \pm 1.29
Late	24.84 \pm 4.44b	38.51 \pm 4.27b	2.86 \pm 0.74b	4.03 \pm 0.82
Herbicide intensity				
Low	32.65 \pm 4.11a	46.09 \pm 5.29	1.36 \pm 0.49	3.73 \pm 0.68
High	43.49 \pm 4.08b	53.25 \pm 5.61	2.01 \pm 0.65	2.91 \pm 0.89
Significance	-----P-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 x HI	0.70	0.83	0.83	0.65

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

Table 2.4. Mean \pm SEM herbivore abundance in experimental plots across fixed effect: oat kill date (early, intermediate, or late) in 2010 and 2011.

	Insect abundance (Mean \pm SEM) ^b			Source of variation		
	Early oat kill date plots	Intermediate oat kill date plots	Late oat kill date plots	Oat kill date		
				Df ^a	F	P
2010 Major Herbivores						
Imported cabbageworm ^{c,f}	5.45 \pm 0.36	9.19 \pm 0.87	8.48 \pm 1.55	2,20	2.26	0.13
Diamondback moth ^{c,f}	16.32 \pm 1.16	14.97 \pm 1.01	16.81 \pm 2.74	2,21	0.79	0.47
Cabbage looper ^c	4.14 \pm 0.50a	7.64 \pm 1.01b	7.38 \pm 1.65ab	2,19	4.72	0.02
Cabbage aphid ^{d,e}	37.08 \pm 2.86	35.16 \pm 3.04	27.66 \pm 2.60	2,23	0.78	0.47
Crucifer flea beetle ^{d,e}	18.60 \pm 1.64a	17.19 \pm 1.61a	23.51 \pm 2.18b	2,25	6.34	<0.01
Onion thrips ^d	55.00 \pm 3.59	67.32 \pm 5.55	49.21 \pm 3.18	2,15	1.40	0.28
2011 Major Herbivores						
Imported cabbageworm ^{c,e}	12.53 \pm 1.00	13.00 \pm 1.00	13.02 \pm 1.13	2,24	0.29	0.75
Diamondback moth ^c	2.82 \pm 0.25	2.23 \pm 0.21	2.09 \pm 0.21	2,18	2.60	0.10
Cabbage looper ^{c,f}	0.08 \pm 0.03a	0.05 \pm 0.03b	0.04 \pm 0.02b	2,26	7.66	<.01
Cabbage aphid ^d	63.56 \pm 8.78	63.44 \pm 12.08	72.50 \pm 11.27	2,15	1.60	0.23
Crucifer flea beetle ^d	76.53 \pm 10.38	77.81 \pm 8.54	75.10 \pm 14.05	2,15	1.44	0.27
Onion thrips ^{d,f}	50.84 \pm 3.12a	79.81 \pm 5.68b	73.95 \pm 4.98ab	2,26	4.40	0.02

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined using model with marketable cabbage yield as a covariate.

^f Abundance determined using model with total predator abundance as a covariate.

Table 2.5. Mean \pm SEM herbivore abundance in experimental plots across fixed effect: herbicide intensity (low or high) in 2010 and 2011.

	Insect abundance (Mean \pm SEM) ^b		Source of variation		
	Low herbicide intensity plots	High herbicide intensity plots	Herbicide intensity		
			df ^a	F	P
2010 Major Herbivores					
Imported cabbageworm ^{c,f}	7.29 \pm 0.59	8.10 \pm 1.06	1,20	0.46	0.51
Diamondback moth ^{c,f}	15.49 \pm 1.15	16.59 \pm 1.87	1,22	1.26	0.27
Cabbage looper ^c	5.35 \pm 0.69a	7.41 \pm 1.13b	1,19	5.88	0.03
Cabbage aphid ^{d,e}	17.34 \pm 1.15a	49.05 \pm 2.67b	1,23	68.98	<0.01
Crucifer flea beetle ^{d,e}	16.61 \pm 1.15	22.81 \pm 1.74	1,25	0.62	0.44
Onion thrips ^d	56.68 \pm 3.99	57.83 \pm 2.96	1,15	0.18	0.67
2011 Major Herbivores					
Imported cabbageworm ^{c,e}	11.70 \pm 0.79a	14.00 \pm 0.91b	1,24	4.44	0.04
Diamondback moth ^c	2.36 \pm 0.19	2.40 \pm 0.18	1,18	1.56	0.23
Cabbage looper ^{c,f}	0.09 \pm 0.03	0.02 \pm 0.01	1,27	0.65	0.43
Cabbage aphid ^d	58.23 \pm 6.16a	74.77 \pm 9.18b	1,15	9.93	<0.01
Crucifer flea beetle ^d	70.61 \pm 9.85	82.36 \pm 10.50	1,32	0.39	0.54
Onion thrips ^{d,f}	70.92 \pm 3.93	65.48 \pm 3.90	1,27	0.27	0.61

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined using model with marketable cabbage yield as a covariate.

^f Abundance determined using model with total predator abundance as a covariate.

Table 2.6. 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) in oat kill date plots ^b			Source of variation		
	Early	Intermediate	Late	Oat kill date		
2010 Major Natural Enemies				df^a	F	P
Spined soldier bug ^c	1.20 \pm 0.44	2.71 \pm 0.69	1.36 \pm 0.28	2,19	1.20	0.32
Pink lady beetle ^{d,e}	0.97 \pm 0.11	0.78 \pm 0.09	1.30 \pm 0.13	2,25	0.15	0.87
14 spotted lady beetle ^d	0.46 \pm 0.07	0.67 \pm 0.09	0.76 \pm 0.09	2,15	1.39	0.28
Lady beetle larvae ^c	0.34 \pm 0.08a	0.33 \pm 0.09a	0.96 \pm 0.17b	2,15	4.26	0.03
Minute pirate bug ^d	5.40 \pm 0.63	4.27 \pm 0.51	3.21 \pm 0.41	2,19	1.74	0.20
Predatory thrips ^d	18.03 \pm 1.50	19.34 \pm 1.91	11.14 \pm 1.15	2,15	1.24	0.32
<i>Cotesia rubecula</i> ^d	10.78 \pm 1.44	6.30 \pm 0.86	6.51 \pm 0.92	2,24	1.33	0.28
Chalcidoidea ^{d,i}	23.78 \pm 1.13a	28.37 \pm 1.23a	37.82 \pm 1.44b	2,24	7.75	< 0.01
2011 Major Natural Enemies						
Spined soldier bug ^c	0.64 \pm 0.21	0.45 \pm 0.17	0.63 \pm 0.27	2,19	0.05	0.95
Pink lady beetle ^{d,e,f,g}	0.76 \pm 0.08a	1.20 \pm 0.12ab	1.51 \pm 0.13b	2,19	5.04	0.02
14 spotted lady beetle ^{d,g}	0.05 \pm 0.01	0.14 \pm 0.03	0.22 \pm 0.04	2,12	2.43	0.11
Convergent lady beetle ^{d,g}	0.11 \pm 0.02ab	0.39 \pm 0.06a	0.09 \pm 0.02b	2,25	4.18	0.03
Lady beetle larvae ^{c,g}	0.08 \pm 0.02	0.19 \pm 0.04	0.38 \pm 0.08	2,20	3.19	0.06
Minute pirate bug ^d	0.84 \pm 0.10	1.63 \pm 0.21	1.50 \pm 0.16	2,18	1.78	0.20
Predatory thrips ^{d,g}	2.48 \pm 0.23a	3.10 \pm 0.30b	3.06 \pm 0.28ab	2,20	5.40	0.01
<i>Cotesia rubecula</i> ^{d,e,h}	1.30 \pm 0.18a	1.32 \pm 0.19ab	1.70 \pm 0.28b	2,24	4.00	0.03
<i>Diadegma insulare</i> ^{d,e}	4.02 \pm 0.66	2.48 \pm 0.50	2.42 \pm 0.54	2,25	1.26	0.25
Chalcidoidea ^{d,g,i}	17.31 \pm 0.77a	21.33 \pm 1.03a	31.88 \pm 2.31b	2,25	8.62	<0.01

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

Table 2.6 (cont'd)

- ^e Abundance determined using model with marketable cabbage yield as a covariate.
- ^f Abundance determined using model with total herbivore abundance as a covariate.
- ^g Abundance determined using model with total predator abundance as a covariate.
- ^h Abundance determined using model with imported cabbageworm abundance as a covariate.
- ⁱ Abundance determined using model with *Cotesia rubecula* abundance as a covariate.

Table 2.7. 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) ^b		Source of variation		
	Low herbicide intensity plots	High herbicide intensity plots	Herbicide intensity		
			df ^a	F	P
2010 Major Natural Enemies					
Spined soldier bug ^c	2.61 \pm 0.52a	0.88 \pm 0.24b	1,19	15.43	<0.01
Pink lady beetle ^{d,e}	1.28 \pm 0.11a	0.75 \pm 0.08b	1,24	18.14	<0.01
14 spotted lady beetle ^d	0.93 \pm 0.08a	0.33 \pm 0.05b	1,15	21.34	<0.01
Lady beetle larvae ^c	0.59 \pm 0.11	0.48 \pm 0.09	1,15	0.84	0.37
Minute pirate bug ^d	6.44 \pm 0.53a	2.20 \pm 0.23b	1,19	23.49	<0.01
Predatory thrips ^d	13.98 \pm 0.97	18.39 \pm 1.53	1,15	0.02	0.88
<i>Cotesia rubecula</i> ^d	6.64 \pm 0.69	9.06 \pm 1.07	1,24	0.71	0.41
Chalcidoidea ^{d,i}	31.75 \pm 1.05a	28.17 \pm 1.15b	1,24	5.58	0.03
2011 Major Natural Enemies					
Spined soldier bug ^c	0.50 \pm 0.18	0.65 \pm 0.17	1,19	0.65	0.43
Pink lady beetle ^{d,e,f,g}	1.25 \pm 0.10	1.07 \pm 0.08	1,20	0.11	0.75
14 spotted lady beetle ^{d,g}	0.13 \pm 0.02	0.14 \pm 0.03	1,22	1.43	0.24
Convergent lady beetle ^{d,g}	0.23 \pm 0.04	0.17 \pm 0.03	1,25	0.29	0.59
Lady beetle larvae ^{c,g}	0.12 \pm 0.02	0.31 \pm 0.06	1,21	4.09	0.06
Minute pirate bug ^d	1.71 \pm 0.17a	0.93 \pm 0.08b	1,18	6.24	0.02
Predatory thrips ^{d,g}	3.22 \pm 0.24	2.54 \pm 0.20	1,20	0.13	0.72
<i>Cotesia rubecula</i> ^{d,e,h}	1.47 \pm 0.18	1.41 \pm 0.18	1,25	4.06	0.06
<i>Diadegma insulare</i> ^{d,e}	2.83 \pm 0.45	3.12 \pm 0.49	1,26	2.98	0.10
Chalcidoidea ^{d,g,i}	23.72 \pm 1.20	23.29 \pm 1.39	1,26	0.77	0.39

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined using model with marketable cabbage yield as a covariate.

^f Abundance determined using model with total herbivore abundance as a covariate.

^g Abundance determined using model with total predator abundance as a covariate.

^h Abundance determined using model with imported cabbageworm abundance as a covariate.

ⁱ Abundance determined using model with *Cotesia rubecula* abundance as a covariate.

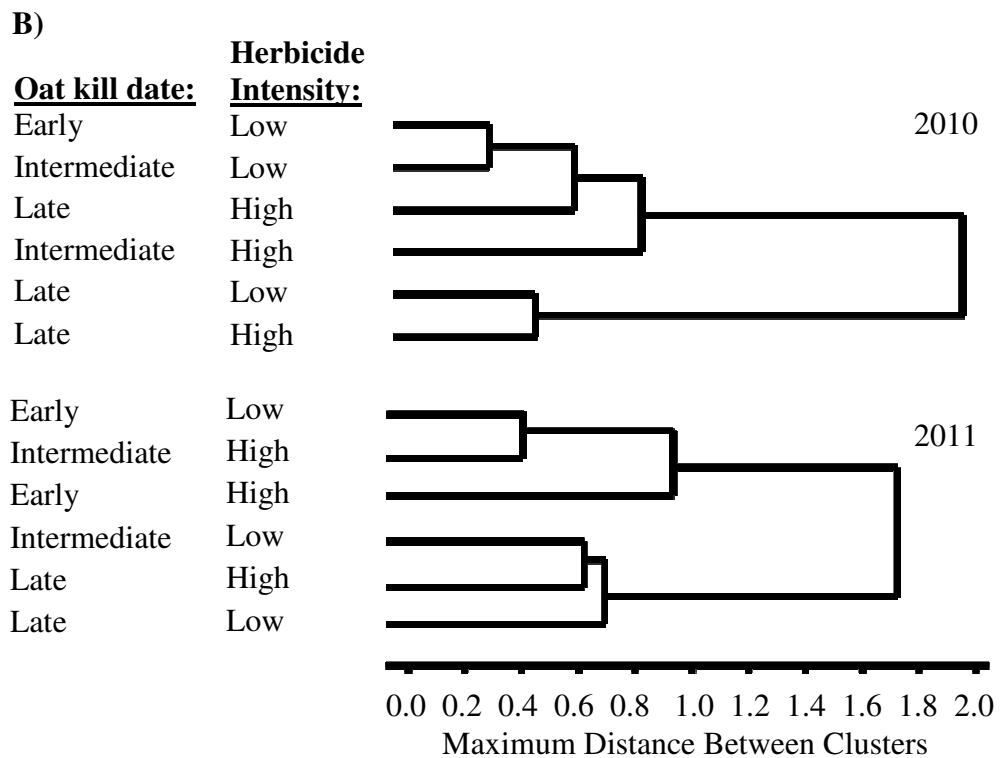
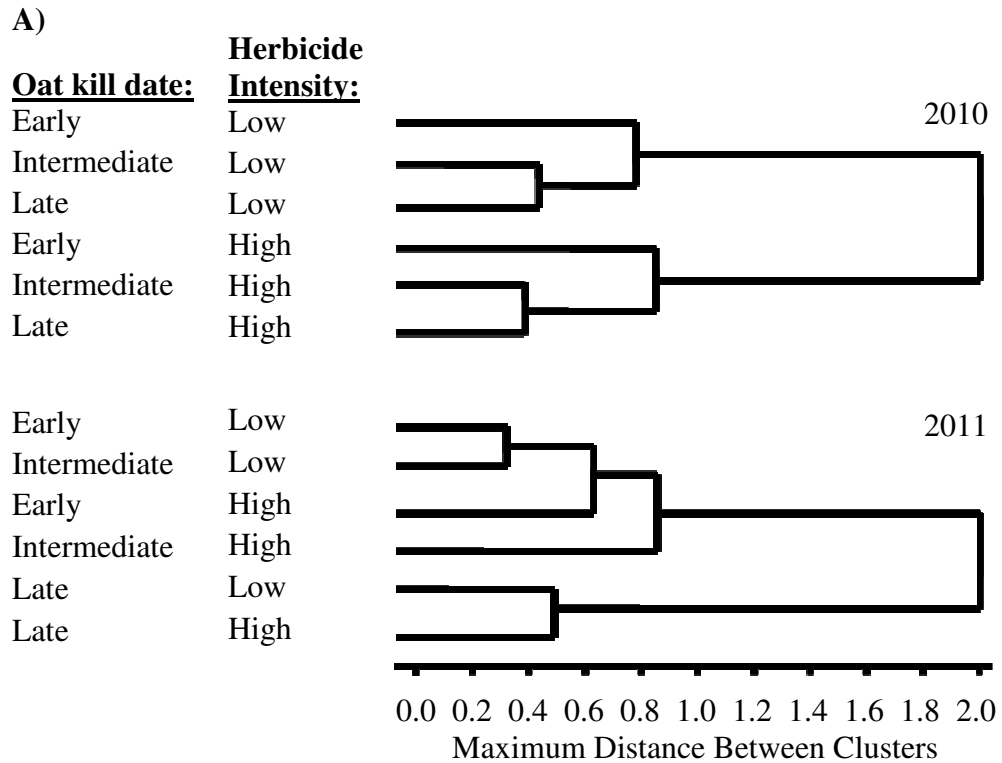


Figure 2.1. Habitat complexity dendrograms based on average linkage distance for the herbivore community (A) and natural enemy community (B) in 2010 and 2011.

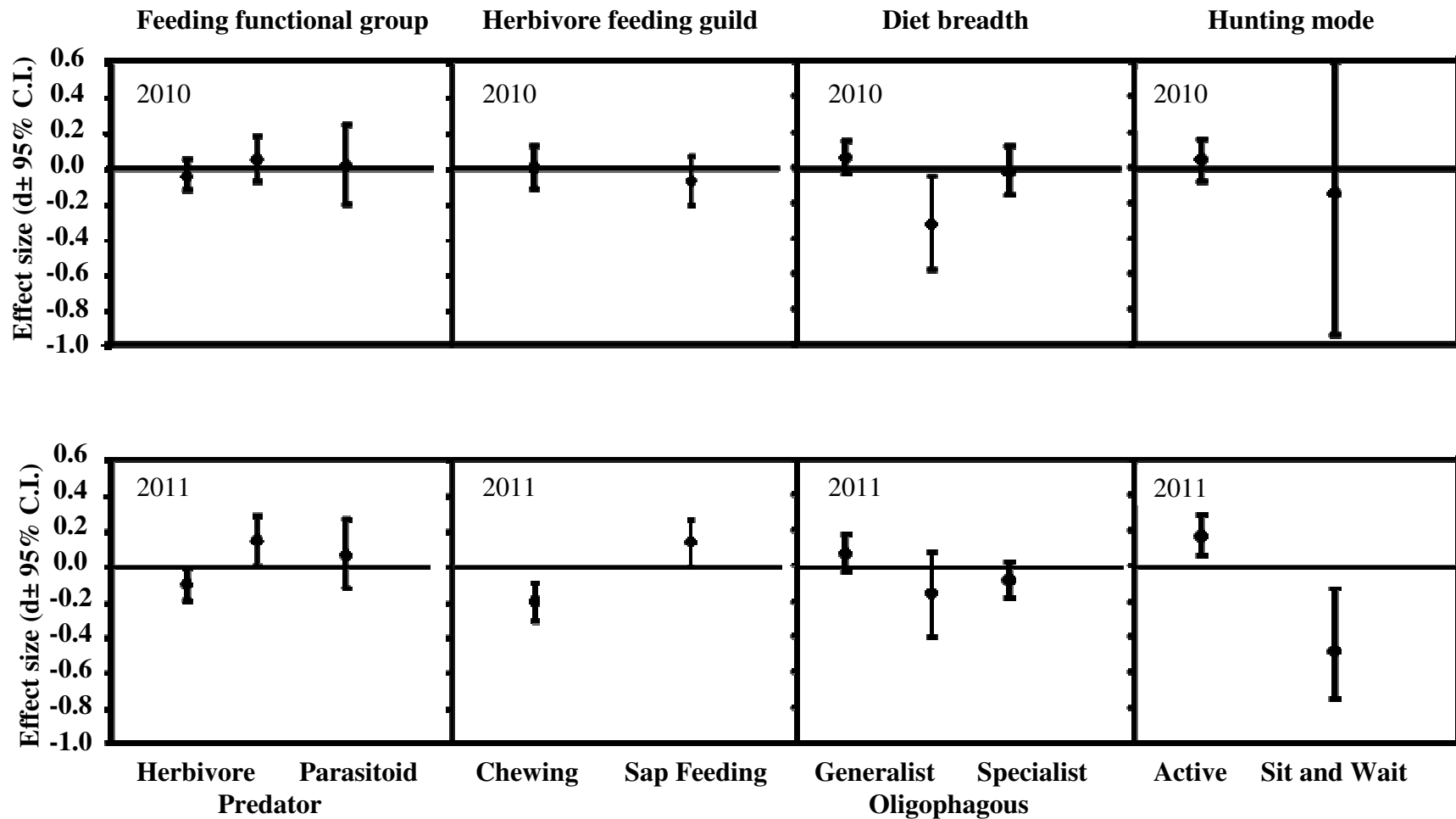


Figure 2.2. Effect of habitat complexity on insect abundance classified according to functional feeding groups, feeding guilds, diet breadth, and hunting modes. Error bars indicate 95% bootstrap confidence intervals. Graphs in the top row are data from 2010, and in the bottom row are from 2011.

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. The effects of habitat complexity between cabbage rows on natural enemy and pest community structure, individual insect species abundance, and insect guilds based on functional traits were investigated.

Insect community structure. Changes in habitat complexity influenced community structure of both herbivore and natural enemies in cabbage. In 2010, herbivore communities were strongly influenced by herbicide intensity (Fig. 2.1A), which affected the abundance of weeds (Table 2.2). In 2011, when weed pressure was lower, herbivore communities were influenced primarily by oat kill date (Fig. 2.1A), which determined the amount of oat mulch between cabbage rows (Table 2.2). 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. 2.1B), which may be the result of natural enemy communities dominated by species that are more responsive to indirect resources such as refuge. In general, these 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, multicolored Asian lady beetle, and the parasitoid, *Diadegma insulare* (Zhao et al. 1992, Harvey and Eubanks 2004, Alhmedi et al. 2009). These insects may be unresponsive to the types of structural or vegetational complexity in this study or to changes at this spatial scale.

Impact of oat kill date on insect abundance. Crucifer flea beetles were positively impacted by the mulch in between rows (Table 2.4), supporting observations by Schellhorn and Sork (1997) in other cole crops in which flea beetles preferred complex and diverse habitats. On the other hand, onion thrips responded negatively to mulching contrary to past observations in mulched onions (Larentzaki et al. 2008).

In 2011, predators such as the pink lady beetle, fourteen spotted lady beetles, lady beetle larvae, and predatory thrips responded positively to the presence of oat mulch in between rows (Table 2.6). Although several of these species have responded similarly to mulching in other crops, such as potato and sweet corn (Brust 1994, Lundgren et al. 2009), my results for predatory thrips and lady beetles, are contrary to results from mulched versus non-mulched onion plots (Larentzaki et al. 2008) and a meta-analysis conducted by Langellotto and Denno (2004).

The positive responses of arthropod abundance to greater mulch in the row-middle may be due to provisioning of shelter, resources, or alternative prey in between rows (Root 1973, Landis et al. 2000, Sunderland and Samu 2000).

In addition to the generalist predators in the cabbage fields, a specialized natural enemy (*Cotesia rubecula*) was positively impacted by the later oat kill date, with greater abundance in 2011 (Table 2.6). Habitat complexity created by non-crop flowering plants can increase *Cotesia*

rubecula parasitism and abundance (Lee and Heimpel 2005), however the effects of non-living habitat are unknown. Although *Cotesia rubecula* wasps rely on chemical cues from host plants and visual cues to find its host (e.g. van Poecke et al. 2003), the greater oat mulch in row middles did not seem to interfere with these cues. The superfamily Chalcidoidea consisting of hyperparasitoids of *D. insulare* and *C. rubecula*, were also more abundant in the plots with later oat kill dates in 2010 and 2011, and lower herbicide intensity in 2010 (Table 2.6, 2.7). Mulching appears to positively influence the third and fourth trophic levels. *Cotesia rubecula* and Chalcidoidea hyperparasitoids may find shelter and attractive microclimates in mulched plots.

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 key herbivore species, the findings of a negative relationship between imported cabbageworm, cabbage aphid, and cabbage looper abundance and herbicide intensity (Table 2.5), 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 due to 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 the spined soldier bug, minute pirate bug, pink lady

beetle, and fourteen spotted lady beetle were more abundant in plots with greater weed pressure in 2010 (Table 2.7).

Although the exact mechanisms for these 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 has been observed in intercropped plots and higher biocontrol in monocultures (Bjorkman et al. 2010, Adati et al. 2011). Complex habitats with non-crop plants such as weeds can host a greater diversity of herbivores, supporting a greater diversity of natural enemies within an agricultural field (Andow 1988). For instance, the weeds and oat mulch in between cabbage rows may be habitat for alternative prey for natural enemies.

Significant covariates for herbivores. In addition to the direct impacts of habitat complexity on arthropod abundance (Figure 1.3), impacts on marketable yield, predator abundance, and abundance of prey or hosts can indirectly influence arthropod abundance across trophic levels (Figure 1.4). Cabbage yield was reduced by later oat kill dates and reduced weed management. The amount of marketable cabbage yield in turn positively influenced cabbage aphids and negatively influenced crucifer flea beetles and imported cabbageworm abundance during this study. Changes in cabbage head size and cabbage quality appear to influence habitat choice for these herbivores. Total predator abundance or the third trophic level influenced abundance of imported cabbageworm, diamondback moth, cabbage loopers, and onion thrips

suggesting predation or changes in predator efficiency may be playing a role in driving prey density in the field. For instance, abundance of the imported cabbageworm was influenced by weed management. Due to the high mobility and egg dispersal of this pest, Banks (1998) has suggested any observed differences in imported cabbageworm abundance across habitats are due to differences in predation. This suggests predation of the imported cabbageworm is lower in the simple habitats with low weed pressures. Since total predator abundance was positively related to imported cabbageworm abundance, total predator abundance does not appear to be a reliable indicator of predation. Perhaps a few key predators are responsible for imported cabbageworm predation.

Significant covariates for natural enemies. Cabbage yield consistently negatively impacted pink lady beetle abundance. Larger cabbage plants may increase hunting time and decrease the lady beetle's hunting efficiency. The quality of odor signals could also have been impacted by cabbage yield or quality, although this was not examined during this study. Total herbivore abundance was only included in the model for the pink lady beetle, suggesting that most generalist predators are not choosing habitats based primarily on prey availability in the field. On the other hand, abundance of *C. rubecula* and its hyperparasitoids were influenced by their respective host's abundance. It is important to note that these specialists appear to follow their hosts around the field and may be relying on odor and visual cues from its hosts, although host searching for *C. rubecula* and the Chalcidoidea hyperparasitoids were not impeded by mulching or weed pressures. Both abundance of generalist predators (e.g. lady beetles and predatory thrips) and specialist parasitoids (e.g. *C. rubecula* and *D. insulare*) were impacted by

total predator abundance suggesting that intraguild predation and interactions within the natural enemy guild could be impacting natural enemy populations in the cabbage field.

Insect functional groups. Research in other agricultural systems (e.g. wheat, canola, cover crops, and corn) and in natural habitats have often 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, while 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, high complexity plots positively influenced predators in 2011, according to a significant positive effect size (Figure 2.2). This appears to support the positive responses of predator abundance to the 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, the high habitat complexity treatments negatively affected chewing

insects, as well as oligophagous and specialized feeders, suggesting that generalist herbivores including sap feeders benefited the most from habitat complexity (Figure 2.2). This trend has also 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 (Batary et al. 2007). In 2011, active hunters were positively influenced by increased habitat complexity and sit and wait hunters were negatively impacted (Figure 2.2). 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 my 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 my 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 treatments, cabbage fields in 2010 and 2011 contained habitats with varying degrees of complexity between rows. This study suggests that greater habitat complexity between cabbage rows can enhance predator populations. However, this complexity reduced cabbage yield, increased populations of a few pests, and enhanced hyperparasitoid abundance, which may reduce the efficiency of the natural enemies in providing effective biological control within the

field. Possible indirect effects of mulching and weed management were also observed, with marketable yield, herbivore abundance, and natural enemy abundance influencing the abundance of individual arthropod species. In particular, cabbage yield and quality, host or prey abundance, and predation appear to play a role in individual species abundance. Cabbage biomass and yields, mid-season and at-harvest respectively, were reduced due to interactions between cabbage, weeds, and oats in 2010. Other studies have also 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 while 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.

CHAPTER 3.

The impact of mulch species and management on natural enemies and biological control in cabbage

Introduction. Cabbage production in the Midwestern United States is threatened by a diverse community of pests, including the imported cabbageworm (*Pieris rapae*, Lepidoptera: Pieridae), diamondback moth (*Plutella xylostella*, Lepidoptera: Plutellidae), cabbage looper (*Trichoplusia ni*, Lepidoptera: Noctuidae), flea beetles (Coleoptera: Chrysomelidae), and aphids (Hemiptera: Aphididae). In cabbage, high levels of predation and parasitism, up to 80% and 50% respectively, have been observed for the imported cabbageworm (Schmaedisk and Shelton 1999, Wold-Burkness et al. 2005). This suggests natural enemies can provide substantial biological control within a cabbage field. Conventional pest management practices, including monocultures and broad-spectrum insecticides can reduce natural enemy populations and reduce the services they provide in vegetables (Bommarco et al. 2011). In contrast, habitat management techniques such as cover cropping have been shown to enhance biological control in vegetables and field crops through the conservation of these natural enemies (Lundgren et al. 2011, Schmidt et al. 2004, Schmidt et al. 2007).

Cover crops are non-harvested plants that provide habitat and resources for natural enemies (Carmona and Landis 1999). When allowed to remain in the cabbage field as living mulch, these plants have been associated with reductions in insect pest abundance (Andow et al. 1986). Past studies have examined other benefits of living mulches and cover crops incorporated in crop rotations such as nutrient uptake (Bath et al. 2006), reductions in nutrient leaching and runoff (Martinez and Guiraud 1990), greater soil health (Teasdale 1998), and weed reduction

(Ilnicki and Enache 1992). Competition between the cover crop and the cash crop has also led to reductions in cabbage yield (Brainard et al. 2004) and limited the adoption of this conservation method.

Killing the cover crop prior to cabbage transplantation may provide an alternative to living mulch. Limiting tillage to planting rows allows killed cover crop mulch to remain on the soil surface. The benefits of cover crop mulch between cabbage rows include reduced soil temperatures and conservation of soil moisture (Schonbeck et al. 1993). Mulching also reduces weed infestations (Bottenberg et al. 1997, Brandsaeter et al. 1998, Franczuk et al. 2010, Masiunas et al. 1997, Zaniewicz-Bajkowska et al. 2009) and can provide weed suppression comparable to herbicide applications (Dillard et al. 2004, Mangan et al. 1995). Effects of cover crop mulching on cabbage yields has been mixed. While several studies have observed decreased cabbage weight (Bottenberg et al. 1997, Brandsaeter et al. 1998, Trdan et al. 2008), mulching has maintained (Haramoto and Brainard 2012) or enhanced cabbage yields in other cases (Franczuk et al. 2010, Riley et al. 2003).

Killed cover crop mulches and other plant residues can reduce diamondback moth, imported cabbageworm, cabbage looper, and aphid abundance in cabbage (Bottenberg et al. 1997, Mangan et al. 1995, Xu et al. 2011). Fewer studies have examined the impact of these management strategies on the natural enemy community. Xu et al. (2011) found greater natural enemy densities in cabbage plots with plant residues present on the soil surface compared to bare soils, suggesting mulching can impact conservation biological control within the field. However, the impact of different mulch species and the management of these mulches on biological control services such as predation and parasitism have not been examined in cabbage.

When choosing cover crops to conserve natural enemies, two groups, legumes and cereal crops, have been more commonly adopted by growers in Michigan and show success in enhancing organic matter, pest management, yield and quality (Snapp et al. 2005). These distinct groups of cover crops have physical or structural differences, which may have diverse impacts on natural enemies through the creation of different types of habitat complexity.

Structural complexity is non-living structure within a habitat that can be manipulated (e.g. surface area, density, height) through the use of different species of cover crop mulches. For instance, legumes are broadleaf plants with greater leaf area than cereal plants. Many legume cover crops (e.g. clovers) grow along the soil surface, providing habitat for arthropods close to the ground. In contrast, many cereal cover crops create greater vertical habitat when allowed to remain standing. Past studies have found that greater structural complexity within a habitat and within a plant enhances natural enemy populations through provisioning of alternative resources, increasing predation efficiency, and providing shelter from intraguild predators (Langellotto and Denno 2004).

Structural complexity can also be manipulated through the management of these cover crops. For example, rolling and crimping reduces cover crop height and the vertical complexity of the habitat between cabbage rows, while creating dense mulch habitat along the soil surface. Studies on management strategies for cover crop mulch have focused on impacts on the first trophic level and abiotic factors, excluding insect pests and natural enemies. For instance, rolling mulch has shown to reduce soil temperatures and has a mixed effect on cabbage yields varying from year to year, while the impact on natural enemies is unknown (Mochizuki et al. 2008). In one case, Laub and Luna (1992) found that reducing cover crop mulch height in corn with mowing (allowing mulch to remain standing) led to greater natural enemy abundance (e.g.

ground dwelling predators) compared to plots with cover crop mulch lying on the soil surface (Laub and Luna 1992). However, mulching management strategies that manipulate habitat height between cabbage rows has never been examined for impacts on biological control.

Monitoring of pest and natural enemy populations in the field provides information on insect diversity and abundance across habitat managements. It does not necessarily explain the mechanism for population reductions and cannot be linked with predation or parasitism rates (Furlong and Zalucki 2010). Sentinel prey studies with natural enemy exclusion cages (Costamagna et al. 2008) can provide predation and parasitism rates provided by guilds of natural enemies. Sentinel prey studies also provide information on the biological control of a specific life stage of the pest species. However, individual natural enemy species providing significant reductions in the pest population cannot be identified with this method.

The goals of this study were to examine the impacts of cover crop species (e.g. legume and cereal) and management (crimped or no crimping) on 1) total arthropod abundance 2) abundance of individual arthropod species and 3) biological control for one of the major cabbage pests in Michigan, the imported cabbageworm. Complex habitats with standing cereal mulch were predicted to positively impact the natural enemy community and individual species. Enhanced biological control was also predicted in these parts of the field.

Materials and Methods

Experimental Design. A field study was established in fall 2011 at the Michigan State University's Horticulture Farm in East Lansing, Michigan. The experiment was a randomized complete block design with six treatments, consisting of combinations of two main effects: mulch species (none, vetch, or rye) and management (none or crimping between rows).

Treatments were replicated four times. Plots (9.14 m x 9.14 m) consisted of 12 rows of cabbage with 76 cm row spacing. Two buffer rows were planted along the edges of the field.

Field Operations. On October 4, 2011 cover crop seeds were broadcast by hand. Winter rye (*Secale cereale*; Dirt Works, New Haven, VT) was broadcast in rye plots at a rate of 183.10 Kg/ha. Hairy vetch (*Vicia villosa*; Johnny's Selected Seeds, Albion, ME) was broadcast in vetch plots at a rate of 61 Kg/ha. On April 27, 2012 Select Max (2.34 L/ha) was applied with a non-ionic surfactant (Dispatch; 1.17 L/ha) to kill the winter rye cover crop. To kill the hairy vetch cover crop, Roundup (3.51 L/ha) was applied on May 11 followed by an application of Stinger (0.58 L/ha), applied on May 22 to effectively kill the vetch cover crop. Due to the dense biomass in vetch plots, vetch plots were mowed using a push mower (DR® Trimmer; Vergennes, VT) reducing vetch biomass and allowing passage of the strip-tiller. On May 29, a Hiniker® Model 6000 two-row strip-tiller (equipped with cutting-coulter, shank-point assembly, and rolling basket) was used to create 25 cm x 25 cm deep strips at 76 cm between-strip spacing. According to soil tests and nutrient management recommendations for cabbage, 345 kg/ha of 19-19-19 (NPK) fertilizer was applied in planting rows at this time (Warncke et al. 2004). Nitrogen was not sidedressed later in the season.

Cover crops were killed prior to strip-tillage. Strip tillage allowed cover crop residue undisturbed in approximately 51 cm between planting rows. After tillage, plots assigned to crimping treatments were crimped by hand using a plywood rectangle (76 x 25 cm) equipped with rope handles. This hand-made crimper effectively knocked over standing mulch in crimped plots.

Cabbage transplants (var. “Blue Dynasty”; Siegers Seed Company, Holland, MI) were grown for 4 wk in 98 cell plug trays and transported to the Horticulture Farm to harden off for 15 d prior to transplanting in the field. Cabbage was transplanted by hand beginning on May 29 into strip-tilled zones (76 cm between rows) with 36 cm between transplants within the row. No fungicides were used. Herbicides included GoalTender 4SC (0.15 L/ha) and Select Max (0.73 L/ha) applied on 10 July across the entire field to manage weeds. By July 8, vetch mulch had decomposed and was no longer visible on the soil surface. To further manage weeds at this time, row middles in vetch plots and plots without mulch were cultivated using a two shank cultivator pulled behind a tractor (John Deere® model 5325; John Deere Company, Moline, IL). An herbicide, GoalTender 4SC (0.44 L/ha), was applied throughout the field and additional hand-weeding was performed in all plots at this time to reduce weed pressure further.

Mulch, weed, and cabbage yield measurements. Mulch height and biomass were measured three times during the growing season on June 18, August 8, and September 4. Mulch height was measured in two 0.25 m² quadrats per plot. Within these randomly placed quadrats, ten height measurements were recorded and mulch biomass was collected. Prior to weighing, all above ground mulch biomass was dried in the oven at 60°C for 7d.

A weed census was also conducted 40d prior to handweeding and 8d and 36d after handweeding. Within the 0.25 m² quadrats, weeds were counted and identified to species. Based on census data, weed abundance and diversity (Shannon-Wiener Index) were calculated. Maximum height for each weed species was also recorded. The most common weed species included: nutsedge (*Cyperus esculentus* L.), common lambsquarters (*Chenopodium album* L.),

smartweed (*Polygonum pensylvanicum* L.), common ragweed (*Ambrosia artemisiifolia* L.), redroot pigweed (*Amaranthus retroflexus* L.), and wild radish (*Raphanus raphanistrum* L.).

Cabbage was harvested beginning on September 5. In each plot, cabbage heads were harvested from the middle 4.57 m of the central 8 rows. The number and weight of marketable and non-marketable heads was also assessed. Cabbage heads greater than 11.4 cm in diameter were considered marketable.

Mulch, weed, and cabbage yield statistical analysis. A mixed model (PROC Mixed, SAS 9.2, 2002-2008) was used to determine the effects of mulch species and management on mulch height, mulch biomass, and cabbage yield. The variable, mulch height was averaged per plot. Mulch biomass and cabbage yield (e.g. biomass and number of marketable and non-marketable heads) were summed per plot. Mulch height, mulch biomass, and cabbage yield were square root transformed ($\sqrt{x + 0.5}$) to meet assumptions of normality and equal variance. An analysis of covariance was performed with a model including mulch species, mulch management, and their interaction as fixed factors and block as a random factor. Weed species height and diversity were included as covariates to determine the impact of these factors on insect abundance and cabbage yield. A least-square means test with Tukey-Kramer adjustment was performed if main effects or their interactions were significant ($\alpha=0.05$).

Arthropod sampling. To determine the effect of mulch species and management on arthropod abundance, Insects were sampled using three sampling methods. First, sessile insects were sampled visually on cabbage plants. Insects were identified and counted on 10 randomly chosen cabbage plants per plot for 11 wk during the growing season. Plants were chosen from

central rows within the plot, eliminating edge effects. All above ground plant tissue was examined during visual sampling.

Highly mobile insects were sampled with yellow sticky traps on metal stakes (7.5×12.3 cm, Great Lakes IPM, Vestaburg, MI) for 10 wk during the growing season. Sticky traps placed 0.4 m from ground level and changed every 7 d.

Ground dwelling arthropods were sampled using pitfall traps 7 times throughout the growing season. Four plastic cups (354.88 ml; Solo Cups, Lake Forest, Illinois) were placed systematically in the central rows of each plot. Traps were submerged in the ground until the brim of the cup was flush with the surface of the soil. These traps remained uncovered for 48 hr before arthropods were removed and identified. All arthropods were identified to species or the lowest possible taxonomic classification (Marshall 2006). Voucher specimens for the imported cabbageworm and major natural enemies were deposited in the A.J. Cook Arthropod Research Collection at Michigan State University (East Lansing, MI).

Arthropod communities. Abundance data from visual, sticky trap, and pitfall sampling was transformed using $\log(x + 0.01)$ to meet assumptions of normality and analyzed using a covariate analysis. Total mobile predators on sticky traps, total ground dwelling predators in pitfall traps, and total parasitoids on sticky traps were examined. Mulch species, mulch management, and the interaction between mulch species and mulch management were fixed factors, block as a random factor, treatment nested within block as the repeated subject (PROC Mixed). Covariates such as weed height, weed diversity, and marketable cabbage yield were included using data at the closest sampling date. A least-square means test with Tukey-Kramer adjustment was performed if main effects were significant ($\alpha=0.05$).

Arthropod abundance. Abundance data from insect sampling was log transformed using $\log(x + 0.01)$ to meet normality assumptions and analyzed with a repeated measures analysis. Impact of treatments on individual herbivore species abundance were examined using on visual sampling and natural enemy data was taken from sticky trap and pitfall trap sampling data. Models included mulch species, mulch management, and the interaction between mulch species and mulch management as fixed factors, date as a repeated factor, block as a random factor, and treatment nested within block as the repeated subject (PROC Mixed). Covariates included weed height, weed diversity, marketable cabbage yield, total herbivore abundance, total predator abundance, total parasitoid abundance, and host abundance. For instance, diamondback moth abundance was included as a covariate for analyzing *Diadegma insulare* abundance and imported cabbageworm abundance was included as a covariate for *Cotesia rubecula* abundance. If main effects were significant ($\alpha=0.05$), we performed least-square means tests with Tukey-Kramer adjustment.

Natural enemy exclusion cages. To determine treatment effects on biological control services provided by different natural enemy guilds (e.g. small predator, large predator, parasitoid), Exclusion cages were placed in the field with sentinel prey. Four exclusion cages were placed in each plot. Each cage consisted of an 8 wk old cabbage plant in a 15.24 x 13.97 cm (diameter x height) pot with Sure-Mix Perlite (Michigan Grower Products, Galesburg, MI). Two 0.91 m wires bent and submerged into the potting soil created a wire framework surrounding the cabbage plant. Four transplanted cabbage plants were randomly selected and replaced by a caged cabbage plant. Each cage was submerged in the soil and leaf pieces with four first instar imported cabbageworm larvae were transferred to the caged plant. Plants were

infested with imported cabbageworm from a greenhouse colony at Michigan State University. Larvae were reared on brussel sprouts (*Brassica oleracea*; Johnny Select Seeds, Albion, ME) with a 16:8 h, L:D photoperiod.

The first cage, excluded all arthropods with a fine white no-see-um netting (0.002 mm² holes, Skeeta Company, Bradenton, FL) closed with a clip at the top of the frame and closed with a rubber band near the bottom of the pot. Any mortality of prey in this cage could be associated with natural mortality due to environmental conditions or handling. The second cage, a mosquito-netting cage, had a white mosquito netting (Skeeta Company, Bradenton, FL) cover instead. This exclusion cage had 2 mm openings, allowing parasitoids and small predators access to the sentinel prey but exclude larger predators, including predatory stink bugs and lady beetles, were excluded. The third cage type, a sham cage, was identical to the mosquito-netting cage. However, the sham cage was not closed with a rubber band at the bottom. The netting was raised 1 cm above the soil surface allowing ground predators access to the sentinel prey. The netting also allowed larger predators access to prey through 10 rectangular openings (3 x 20 cm) in two rings around the netting. The sham cage accounts for any effects of the presence of netting on insect movement. The final cage, an open control cage lacked any netting allowing movement of any size natural enemy into the cage.

Cages were placed in the field for a 36 h period before retrieval. After 36 h, predators were removed from cages and plants were re-covered with a fine mesh. Any remaining imported cabbageworm larvae were reared on cabbage plants until pupating into an adult butterfly or a parasitoid pupa or adult was observed. Predation and parasitism rates were calculated based on larvae killed or parasitized. The exclusion cage experiment was repeated three times during the growing season starting on June 28, July 30, and August 23.

Mortality and parasitism rates were transformed using $\sqrt{x + 0.5}$ to meet assumptions for normality and analyzed using an analysis of variance with block as a random factor, treatment nested within block as the subject, and mulch species, mulch management, cage type, and the interactions of these variables as fixed factors (PROC Mixed). A least-square means test with Tukey-Kramer adjustment was performed if main effects were significant ($\alpha=0.05$).

Results

Mulch, weed, and cabbage yield measurements. Mulch height was significantly impacted by mulch species, mulch management, and the interaction between these factors throughout the cabbage growing season (Table 3.1). At an early, intermediate, and late date in the growing season, mulch height in rye plots were significantly higher than vetch ($t > 7.40$, $df = 15$, $P < 0.02$) or bare soil plots ($t > 7.40$, $df = 15$, $P < 0.01$). Mulch height in vetch plots was not significantly different from bare soil plots throughout the growing season ($t = 1.88$, $df = 15$, $P > 0.08$). Throughout the summer, plots without crimping contained taller mulch than crimped plots ($t > 2.54$, $df = 15$, $P < 0.02$). However, only rye plots contained lower mulch in crimped plots compared to non-crimped plots ($t > 4.40$, $df = 15$, $P < 0.01$). Rye mulch was approximately three, 11, and four times taller in non-crimped compared to crimped plots during the early, intermediate, and late portions of the season respectively.

Mulch management (crimping) and the interaction between mulch species and management did not affect mulch biomass (Table 3.1). However, mulch biomass differed across mulch species treatments (Table 3.1), with the greatest amount of biomass in rye plots throughout the growing season. During the early, intermediate, and late parts of the season, approximately two, 21, and 18 times greater biomass was recorded in rye plots than vetch plots.

Mulch management did not influence weed height, weed abundance, or weed species richness ($F < 1.18$, $df = 1, 18$, $P > 0.29$). However, weed height was significantly reduced in plots with rye mulch (Table 3.2), with weed height in rye plots 48% and 40% lower than bare soil and vetch plots respectively ($t = 2.75$, $df = 18$, $P < 0.03$). Weed abundance and species richness were 2 times and 50% greater in bare soil plots respectively compared to rye mulch plots ($t > 3.19$, $df = 15$, $P < 0.02$).

Cabbage yields at harvest were divided into marketable and non-marketable yields (Table 3.3, Supp Table S4). The covariates, weed height and diversity, during the early, intermediate, and late sampling date were not significant and therefore were excluded from the cabbage yield models. Mulch management did not significantly affect cabbage yields ($t < 0.28$, $df = 15$, $P > 0.96$), but marketable yield was two times greater in bare soil and vetch plots compared to plots with rye mulch ($t > 2.57$, $df = 15$, $P < 0.05$). In contrast, non-marketable yields were greatest in rye plots with 1.5 times more cabbage biomass compared to bare soil or vetch plots ($t > 3.11$, $df = 15$, $P < 0.02$).

The number of marketable and non-marketable cabbage heads did not differ across mulch management treatments. However, the number of cabbage heads was significantly different across mulch species (Supp Table S4). Bare soil plots contained the greatest number of marketable cabbage heads, with two times more heads than rye plots ($t = 3.31$, $df = 15$, $P = 0.01$). Alternatively, rye plots contained the greatest number of non-marketable cabbage heads, with 1.5 times more cabbage heads than bare soil plots ($t = 3.13$, $df = 15$, $P = 0.02$). The number of marketable or non-marketable cabbage heads in vetch plots was not significantly different from the other treatments ($t < 2.39$, $df = 15$, $P > 0.07$).

Arthropod communities. Weed diversity affected total mobile predator abundance on July 1, July 23, and August 11 ($F > 5.41$; $df = 1, 24$; $P < 0.03$). Neither weed diversity nor weed height were significant covariates for total ground predator or total parasitoid abundance and were excluded from both models.

Trends were not consistent for total mobile predators, ground predators, or parasitoids throughout the growing season, suggesting a limited impact of habitat complexity on total natural enemy abundance. For instance, on July 1, mobile predators were 51% more abundant in bare soil plots compared to rye plots ($t > 3.16$, $df = 24$, $P < 0.01$). However, on June 18 and August 11, predators were 86 and 33% more abundant in rye plots compared to bare soil ($t > 3.16$, $df = 24$, $P < 0.01$). Mulch management was significant on June 26, July 16, and August 16 ($F > 7.62$; $df = 1, 20$; $P < 0.02$) with 27 and 49% more predators in non-crimped plots in June 26 and July 16 ($t > 2.76$, $df = 20$, $P < 0.02$), while crimped plots contained 67% more predators on August 16 ($t = 2.81$, $df = 19$, $P = 0.01$).

Total ground predator abundance significantly differed among treatments at the end of the season on the August 30 sampling date (Figure 3.2). Total ground beetle abundance in rye plots without crimping was more than 8 times greater than vetch plots without crimping ($t = 4.45$, $df = 15$, $P < 0.01$) and crimped bare soil plots ($t > 3.44$, $df = 15$, $P = 0.04$).

Trends in total parasitoid abundance were not consistent throughout the season. For instance, plots with rye or vetch mulch contained 62 and 51% more parasitoids than bare soil plots ($t > 2.99$, $df = 15$, $P < 0.02$). On July 16 total parasitoid abundance differed among mulch management ($F = 11.58$; $df = 1, 12$; $P < 0.01$) with 26% fewer parasitoids in crimped compared to non crimped plots ($t = -3.40$, $df = 12$, $P < 0.01$). Although bare soil crimped plots contained remarkably high parasitoid abundance compared to other treatments on July 1 and 10, parasitoid

abundance was not significantly higher in these plots across mulch species ($F < 1.26$; $df = 2,15$; $P > 0.31$), mulch management ($F < 2.78$; $df = 1,15$; $P > 0.12$), or the interaction between species and management ($F < 2.70$; $df = 2,15$; $P > 0.10$). A group of gregarious pupal parasitoids (Chalcidoidea) accounted for 72-99% of the parasitoids on these two sampling dates. However, abundance of this species ranged greatly (38-385 individuals per plot). In particular, a single experimental plot in the corner of the field contained 385 and 343 individuals of this species on July 1 and 10 accounting for the spike in parasitoid abundance.

Arthropod abundance. Since interactions between main effects were not significant, only main effects are presented here. Mulch management did not affect the abundance of pests such as the imported cabbageworm, diamondback moth, cabbage looper, cabbage aphid, crucifer flea beetle, and onion thrips (Table 3.5). One pest, the striped flea beetle, was 13% more abundant in non-crimped plots compared to crimped plots ($t = 2.63$, $df = 21$, $P = 0.02$). Abundance of a single natural enemy species, the fourteen spotted lady beetle, also differed across mulch management (Table 3.6). This predator was 2.5 times more abundant in crimped compared to non-crimped plots ($t = 2.57$, $df = 20$, $P = 0.03$).

While most pests did not respond to mulch species, the imported cabbageworm (Table 3.7) were 20% more abundant in rye compared to hairy vetch plots ($t = 5.10$, $df = 21$, $P < 0.01$) and 19% more abundant in rye compared to bare soil plots ($t = 4.91$, $df = 23$, $P < 0.01$).

Mulch species affected the abundance of several natural enemy species (Table 3.8). Three natural enemies were negatively impacted by the presence of rye mulch, including the pink lady beetle, and *Poecilus* sp. ground beetles other than *Poecilus chalcites*. The pink lady beetle was 16% and 33% more abundant in bare soil ($t = 2.94$, $df = 28$, $P < 0.01$) and hairy vetch plots ($t =$

2.19, $df = 27$, $P = 0.04$) respectively, compared to plots with rye mulch. Ground beetles in the genus *Poecilus*, excluding the common *Poecilus chalcites* species, were seven and three times more abundant in bare soil ($t = 5.30$, $df = 27$, $P < 0.01$) and hairy vetch plots ($t = 3.26$, $df = 23$, $P < 0.01$) respectively, compared to rye plots.

Five natural enemies were positively impacted by the presence of rye mulch, including four generalist predators (*Harpalus pennsylvanicus*, *Pterostichus permundus*, and spiders in the family Linyphiidae) and a specialist parasitoid, *Cotesia rubecula*. The ground beetle *Harpalus pennsylvanicus* was nearly three times and five times more abundant in rye plots compared to hairy vetch ($t = 4.42$, $df = 18$, $P < 0.01$) and bare soil plots ($t = 7.15$, $df = 22$, $P < 0.01$) respectively. The ground beetle *Pterostichus permundus* was nearly six times and 15 times more abundant in rye plots compared to hairy vetch ($t = 6.09$, $df = 21$, $P < 0.01$) and bare soil plots ($t = 5.66$, $df = 25$, $P < 0.01$) respectively. A group of spiders in the family Linyphiidae commonly referred as sheet weaver spiders were more than five times and two times more abundant in rye plots compared to bare soil ($t = 4.54$, $df = 22$, $P < 0.01$) and hairy vetch plots ($t = 3.18$, $df = 18$, $P < 0.01$) respectively. The specialist parasitoid, *Cotesia rubecula*, was approximately two times more abundant in rye plots compared to plots with bare soil ($t = 5.85$, $df = 26$, $P < 0.01$) and 34% more abundant in rye plots compared to vetch ($t = 4.72$, $df = 24$, $P < 0.01$).

Significant covariates for herbivores. Weed height was a significant covariate for the imported cabbageworm, diamondback moth, cabbage looper, and striped flea beetle ($F = 15.85$, $P < 0.01$) positively influencing herbivore abundance, although the imported cabbageworm was negatively influenced by greater weed height. Weed diversity negatively impacted cabbage looper and cabbage aphid abundance, and positively influenced crucifer flea beetle abundance (F

> 6.43, $P < 0.01$). Marketable cabbage yield positively impacted a single herbivore, the diamondback moth ($F = 8.24$, $df = 1,22$, $P < 0.01$). Total predator abundance positively impacted the imported cabbageworm and cabbage looper, and negatively influenced the diamondback moth ($F > 8.45$, $P < 0.01$). Total parasitoid abundance positively impacted the imported cabbageworm ($F = 129.36$, $df = 1,257$, $P < 0.01$).

Significant covariates for natural enemies. Weed height positively influenced the pink lady beetle and negatively influenced *C. rubecula* ($F > 34.68$, $P < 0.01$). Weed diversity positively impacted the spined soldier bug, minute pirate bug, and Lycosids, and negatively impacted *Cyclotrachelus sodalist* and *Pterostichus permundus* ($F > 6.43$, $P < 0.01$). Marketable cabbage yield significantly impacted *Cyclotrachelus sodalist* negatively and *Anisodactylus sanctaecrucis* abundance positively ($F > 7.55$, $P < 0.01$). Total herbivore abundance was not a significant covariate for any natural enemies, however total predator abundance significantly impacted the ground dwelling arthropods: *B. quadrimaculatum*, *Poecilus sp.*, *Scarites quadriceps*, *Anisodactylus sanctaecrucis*, *Harpalus pennsylvanicus*, *Amara sp.*, *Cicindela sp.*, Staphylinidae, Centipede, Lycosidae, and Phalangidae. As in 2010 and 2011, *Cotesia rubecula* and its hyperparasitoids were positively impacted by abundance of their hosts ($F > 3.84$, $P < 0.05$).

Natural enemy exclusion cages.

Mortality. Mortality rates of the imported cabbageworm were not significantly different across the interactions between cage types and mulch species ($F < 1.49$; $df = 6,54$; $P > 0.20$) or cage types and mulch management ($F < 0.63$; $df = 3,54$; $P > 0.60$). This suggests larval mortality

due to different natural enemy guilds was unaffected by mulch species or management treatments. Predation by small and large predators is suspected to be similar across treatments.

However, mortality rates were significantly different across cage types at each sampling date ($F > 18.51$; $df = 3,54$; $P < 0.01$) (Figure 3.4). The no-see-um netting cages effectively excluded all natural enemies with mortality rates between 1-5% during the season (Figure 3.4). Predators and parasitoids were not observed inside the cages, suggesting loss of larvae were due to natural mortality rather than actual predation. Throughout the season, mortality rates were significantly lower in no-see-um cages compared to the other cage types ($t > 5.41$, $df = 54$, $P < 0.01$) with mortality rates ranging from 43-89%. Corpses were rarely recovered; this suggests mortality may be due to movement of larvae off the plant in addition to consumption of the first instar larvae. During the early, intermediate, and late part of the growing season, mortality rates in the mosquito netting cage that excluded large predators, were not significantly different from the sham or no-netting cages ($t < 1.59$, $df = 54$, $P > 0.12$) that allowed all natural enemies access to the prey, suggesting the majority of larval predation is due to the small predator guild.

Parasitism. The interaction between cage type and mulch species ($F < 2.13$; $df = 6,54$; $P > 0.06$) or cage type and mulch management treatments ($F < 1.34$; $df = 3,54$; $P > 0.27$) did not affect the percent of parasitized imported cabbageworm. This suggests different sizes of parasitoids responded similarly across treatments and mulch species or management did not enhance parasitism by a particular guild of parasitoids.

The no-see-um netting cage effectively excluded parasitoids, with 0% parasitism observed at each sampling date (Figure 3.5). During the early part of the season, parasitism rates did not differ across cage type ($F = 2.13$; $df = 3,54$; $P = 0.11$). However, later in the growing

season, mortality rates were significantly different across cage types ($F > 8.59$; $df = 3,54$; $P < 0.01$). During the intermediate and late season sampling dates, parasitism rates in the mosquito, sham, and no-netting cages ($t > 3.24$, $df = 54$, $P < 0.01$) which allowed parasitoids access to the larvae, were significantly greater than the no-see-um cages which excluded the parasitoids. Parasitism rates ranged from 18-25% later in the growing season.

Table 3.1. Mean \pm SEM mulch height at an early, intermediate, and late date during the growing season.

Main effects	Mulch height (cm) ^{a,b}		
	Early season	Intermediate Season	Late season
Treatment			
Bare soil / no crimping	0.00 \pm 0.00c	0.00 \pm 0.00c	0.00 \pm 0.00b
Hairy vetch / no crimping	1.53 \pm 0.21c	0.38 \pm 0.13bc	0.00 \pm 0.00b
Winter rye / no crimping	34.18 \pm 8.18a	11.18 \pm 2.03a	5.95 \pm 1.81a
Bare soil / crimping	0.00 \pm 0.00bc	0.00 \pm 0.00c	0.00 \pm 0.00b
Hairy vetch / crimping	1.52 \pm 0.35bc	0.40 \pm 0.14bc	0.00 \pm 0.00b
Winter rye / crimping	10.21 \pm 3.90b	1.36 \pm 0.33b	1.52 \pm 0.21b
Significance	-----P-value-----		
Mulch species (S)	<0.01	<0.01	<0.01
Mulch management (M)	0.01	<0.01	0.03
S x M	<0.01	<0.01	0.01

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

^b These represent average mulch heights within the sampling quadrats.

^c These represent total mulch biomass within the sampling quadrats.

Table 3.2. Mean \pm SEM mulch biomass at an early, intermediate, and late date during the growing season.

Main effects	Mulch biomass (g/m^2) ^{a,c}		
	Early season	Intermediate Season	Late season
Mulch species			
Bare soil	0.00 \pm 0.00a	0.00 \pm 0.00a	0.00 \pm 0.00a
Hairy vetch	23.91 \pm 4.19b	1.72 \pm 0.44b	2.32 \pm 1.07b
Winter rye	47.53 \pm 9.17c	36.16 \pm 6.41c	41.35 \pm 8.80c
Mulch management			
No crimping	24.84 \pm 7.46	10.69 \pm 4.35	15.00 \pm 7.89
Crimped	22.79 \pm 7.46	14.56 \pm 6.95	14.11 \pm 6.04
Significance	-----P-value-----		
Mulch species (S)	<0.01	<0.01	<0.01
Mulch management (M)	0.62	0.47	0.61
S x M	0.94	0.68	0.36

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

^b These represent average mulch heights within the sampling quadrats.

^c These represent total mulch biomass within the sampling quadrats.

Table 3.3. Mean \pm SEM weed height, weed abundance, and weed species richness across mulch species and management in 2012.

Main effects	Weed height (cm) ^a	Weed abundance (per m ²) ^a	Weed species richness (per m ²) ^a
Mulch species			
Bare soil	6.23 \pm 1.04a	12.83 \pm 2.39a	3.75 \pm 0.31a
Hairy vetch	5.45 \pm 0.92a	9.83 \pm 1.50ab	3.38 \pm 0.36ab
Winter rye	3.25 \pm 0.67b	4.67 \pm 0.83b	2.50 \pm 0.32b
Mulch management			
No crimping	4.98 \pm 0.77	8.14 \pm 1.06	3.28 \pm 0.29
Crimped	4.98 \pm 0.73	10.08 \pm 1.80	3.14 \pm 0.28
Significance	-----P-value-----		
Mulch species (S)	< 0.01	< 0.01	0.02
Mulch management (M)	0.99	0.29	0.67
S x M	0.53	0.26	0.39

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

Table 3.4. Mean \pm SEM non-marketable and marketable fresh weight of cabbage heads at harvest.

Main effects	Marketable (kg) ^a	Non-marketable (kg) ^a
Mulch species		
Bare soil	31.47 \pm 5.46a	17.20 \pm 2.85a
Hairy vetch	30.25 \pm 4.71a	17.50 \pm 1.99a
Winter rye	15.54 \pm 3.21b	28.25 \pm 1.59b
Mulch management		
No crimping	25.92 \pm 4.42	20.77 \pm 2.23
Crimped	25.58 \pm 4.05	21.20 \pm 2.45
Significance	-----P-value-----	
Mulch species (S)	0.03	<0.01
Mulch management (M)	0.94	0.93
S x M	0.12	0.44

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

Table 3.5. Herbivore abundance in experimental plots across fixed effect: mulch management (no crimping or crimped).

	Insect abundance (Mean \pm SEM) ^b		Source of variation		
	No crimping plots	Crimping plots	Mulch management		
			df ^a	<i>F</i>	<i>P</i>
Major Herbivores					
Imported cabbageworm ^{c,e,h,i}	16.93 \pm 0.96	16.64 \pm 0.91	1,19	1.27	0.27
Diamondback moth ^{c,e,g,h}	1.03 \pm 0.11	1.11 \pm 0.11	1,20	0.02	0.89
Cabbage looper ^{c,e,f,h}	1.58 \pm 0.14	1.73 \pm 0.17	1,22	0.17	0.68
Cabbage aphid ^{d,f}	37.53 \pm 2.07	40.47 \pm 2.79	1,22	0.55	0.47
Crucifer flea beetles ^{d,f}	18.75 \pm 1.89	28.94 \pm 3.93	1,21	0.82	0.38
Striped flea beetles ^{d,e}	14.71 \pm 0.93a	12.97 \pm 0.93b	1,22	6.89	0.02
Onion thrips ^d	130.81 \pm 8.02	131.14 \pm 7.60	1,19	0.04	0.84

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined using model with weed height as a covariate

^f Abundance determined using model with weed diversity as a covariate

^g Abundance determined using model with marketable cabbage yield as a covariate.

^h Abundance determined using model with total predator abundance as a covariate.

^I Abundance determined using model with total parasitoid abundance as a covariate.

Table 3.6. Natural enemy abundance in experimental plots across fixed effect: mulch management (no crimping or crimped).

	Insect abundance (Mean \pm SEM) ^b		Source of variation		
	No crimping	Crimping	Mulch management		
Major Natural Enemies			Df ^a	F	P
Spined soldier bug ^{c,g}	1.21 \pm 0.18	1.06 \pm 0.16	1,20	0.75	0.40
Pink lady beetle ^{d,f}	2.58 \pm 0.20	2.66 \pm 0.26	1,20	0.12	0.73
14 spotted lady beetle ^d	0.09 \pm 0.02a	0.25 \pm 0.04b	1,21	6.55	0.02
Convergent lady beetle ^d	0.12 \pm 0.02	0.12 \pm 0.02	1,15	0.00	1.00
Minute pirate bug ^{d,g}	4.25 \pm 0.34	4.10 \pm 0.36	1,25	0.68	0.42
Predatory thrips ^d	5.06 \pm 0.32	5.16 \pm 0.36	1,18	0.08	0.78
<i>B. quadrimaculatum</i> ^{e,f,l}	1.81 \pm 0.27	1.54 \pm 0.23	1,23	1.76	0.20
<i>Poecilus sp.</i> ^{e,g,l}	0.58 \pm 0.11	0.43 \pm 0.09	1,21	0.15	0.71
<i>Poecilus chalcites</i> ^{e,f,l}	0.42 \pm 0.11	0.21 \pm 0.05	1,20	0.68	0.42
<i>Cyclotrachelus sodalis</i> ^{e,g,h}	0.15 \pm 0.05	0.17 \pm 0.04	1,17	0.91	0.35
<i>Scarites quadriceps</i> ^{e,l}	0.33 \pm 0.09	0.32 \pm 0.07	1,15	0.35	0.56
<i>A. sanctaecrucis</i> ^{e,h,l}	0.19 \pm 0.06	0.05 \pm 0.01	1,15	1.47	0.24
<i>Harpalus pennsylvanicus</i> ^l	2.65 \pm 0.40	3.11 \pm 0.47	1,19	1.51	0.23
<i>Harpalus erraticus</i> ^e	0.10 \pm 0.03	0.11 \pm 0.03	1,17	0.00	0.97
<i>Amara sp.</i> ^{e,l}	0.10 \pm 0.02	0.11 \pm 0.03	1,16	0.01	0.93
<i>Pterostichus permundus</i> ^{e,g}	0.12 \pm 0.03	0.12 \pm 0.04	1,18	0.17	0.69
<i>Cicindela sp.</i> ^{e,l}	0.05 \pm 0.02	0.24 \pm 0.08	1,18	1.05	0.32
Staphylinidae ^{e,l}	0.26 \pm 0.05	0.29 \pm 0.06	1,19	0.02	0.88
Centipede ^{e,l}	0.05 \pm 0.02	0.07 \pm 0.02	1,20	1.42	0.25
Lycosidae ^{e,g,l}	2.14 \pm 0.21	2.25 \pm 0.24	1,24	1.14	0.30
Linyphidae ^e	0.23 \pm 0.06	0.18 \pm 0.04	1,18	0.02	0.90
Phalangidae ^{e,f,l}	3.30 \pm 0.57	3.67 \pm 0.66	1,23	1.06	0.31
<i>Cotesia rubecula</i> ^{d,f,j}	6.30 \pm 0.93	7.10 \pm 0.49	1,19	0.02	0.88
<i>Diadegma insulare</i> ^d	0.63 \pm 0.06	0.82 \pm 0.14	1,20	0.04	0.85
Chalcidoidea ^{d,k}	46.44 \pm 1.92	49.1 \pm 3.13	1,24	0.16	0.69

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined from pitfall trap abundance per plot.

^f Abundance determined using model with weed height as a covariate.

Table 3.6 (cont'd)

^g Abundance determined using model with weed diversity as covariate.

^h Abundance determined using model with marketable cabbage yield as a covariate.

ⁱ Abundance determined using model with total herbivore abundance as a covariate.

^j Abundance determined using model with imported cabbageworm abundance as a covariate.

^k Abundance determined using model with total predator abundance as a covariate.

Table 3.7. Herbivore abundance in experimental plots across fixed effect: mulch species (bare soil, hairy vetch, rye).

	Insect abundance (Mean \pm SEM) ^b			Source of variation		
	Bare soil	Hairy vetch	Rye	Mulch species		
				df ^a	<i>F</i>	<i>P</i>
Major Herbivores						
Imported cabbageworm ^{c,e,h,i}	15.81 \pm 0.37a	15.74 \pm 1.15a	18.81 \pm 1.20b	2,22	5.72	0.01
Diamondback moth ^{c,e,g,h}	1.03 \pm 0.12	1.24 \pm 0.16	0.94 \pm 0.10	2,20	1.01	0.38
Cabbage looper ^{c,e,f,h}	1.66 \pm 0.18	1.52 \pm 0.17	1.78 \pm 0.22	2,24	2.19	0.13
Cabbage aphid ^{d,f}	35.14 \pm 2.87	41.38 \pm 3.21	40.61 \pm 2.96	2,63	1.51	0.22
Crucifer flea beetles ^{d,f}	31.53 \pm 5.13	29.41 \pm 3.63	10.05 \pm 0.95	2,22	0.10	0.91
Striped flea beetles ^{d,e}	14.50 \pm 1.27	14.04 \pm 1.15	12.93 \pm 1.00	2,25	1.47	0.25
Onion thrips ^d	124.71 \pm 9.33	144.41 \pm 10.84	123.61 \pm 8.21	2,19	3.58	0.05

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined using model with weed height as a covariate

^f Abundance determined using model with weed diversity as a covariate

^g Abundance determined using model with marketable cabbage yield as a covariate.

^h Abundance determined using model with total predator abundance as a covariate.

ⁱ Abundance determined using model with total parasitoid abundance as a covariate.

Table 3.8. Natural enemy abundance in experimental plots across fixed effect: mulch species (bare soil, hairy vetch, rye).

	Insect abundance (Mean \pm SEM) ^b			Source of variation		
	Bare soil	Hairy vetch	Rye	Mulch species		
Major Natural Enemies				df ^a	F	P
Spined soldier bug ^{c,g}	1.19 \pm 0.20	1.14 \pm 0.20	1.08 \pm 0.21	2,82	2.27	0.11
Pink lady beetle ^{d, f}	2.61 \pm 0.25a	2.99 \pm 0.37a	2.25 \pm 0.18b	2,27	4.59	0.02
14 spotted lady beetle ^{d,f,g}	0.21 \pm 0.04a	0.23 \pm 0.04a	0.07 \pm 0.02b	2,20	3.06	0.07
Convergent lady beetle ^d	0.13 \pm 0.03	0.11 \pm 0.03	0.11 \pm 0.03	2,15	0.01	0.99
Minute pirate bug ^{d,g}	4.70 \pm 0.45	4.87 \pm 0.50	2.89 \pm 0.28	2,26	2.51	0.10
Predatory thrips ^d	4.51 \pm 0.40	4.62 \pm 0.33	6.25 \pm 0.50	2,18	3.50	0.05
<i>B. quadrimaculatum</i> ^{e,f,l}	1.46 \pm 0.29	1.89 \pm 0.33	1.65 \pm 0.30	2,90	1.74	0.18
<i>Poecilus sp.</i> ^{e,f,l}	0.95 \pm 0.19a	0.44 \pm 0.09b	0.13 \pm 0.04c	2,23	14.45	<0.01
<i>Poecilus chalcites</i> ^{e,f,l}	0.20 \pm 0.07a	0.25 \pm 0.08a	0.51 \pm 0.14b	2,22	1.94	0.06
<i>Cyclotrachelus sodalis</i> ^{e,g,h}	0.09 \pm 0.04	0.18 \pm 0.06	0.22 \pm 0.06	2,17	1.00	0.39
<i>Scarites quadriceps</i> ^{e,l}	0.39 \pm 0.11	0.25 \pm 0.07	0.35 \pm 0.11	2,15	0.25	0.78
<i>A. sanctaecrucis</i> ^{e,h,l}	0.16 \pm 0.08	0.11 \pm 0.04	0.09 \pm 0.04	2,15	0.14	0.87
<i>Harpalus pennsylvanicus</i> ^l	1.13 \pm 0.20a	2.07 \pm 0.32b	5.51 \pm 0.81c	2,22	23.91	<0.01
<i>Harpalus erraticus</i> ^e	0.04 \pm 0.02	0.09 \pm 0.04	0.16 \pm 0.04	2,17	2.15	0.15
<i>Amara sp.</i> ^{e,l}	0.07 \pm 0.02	0.09 \pm 0.04	0.15 \pm 0.04	2,16	2.62	0.10
<i>Pterostichus permundus</i> ^{e,g}	0.05 \pm 0.03a	0.02 \pm 0.03a	0.29 \pm 0.06b	2,18	17.85	<0.01
<i>Cicindela sp.</i> ^{e,l}	0.09 \pm 0.04	0.16 \pm 0.08	0.18 \pm 0.10	2,18	0.01	0.99
Staphylinidae ^{e,l}	0.18 \pm 0.06	0.40 \pm 0.08	0.24 \pm 0.06	2,19	2.93	0.08

Table 3.8 (cont'd)

	Insect abundance (Mean \pm SEM) ^b			Source of variation		
	Bare soil	Hairy vetch	Rye	df ^a	F	P
Major Natural Enemies						
Centipede ^{e,l}	0.11 \pm 0.04	0.02 \pm 0.01	0.05 \pm 0.03	2,20	1.47	0.25
Lycosidae ^{e,g,l}	2.14 \pm 0.29	2.47 \pm 0.25	1.96 \pm 0.27	2,25	2.07	0.15
Linyphidae ^e	0.07 \pm 0.02a	0.18 \pm 0.05a	0.36 \pm 0.08b	2,18	10.71	<0.01
Phalangidae ^{e,f,l}	3.50 \pm 0.71	3.60 \pm 0.76	3.35 \pm 0.79	2,23	1.83	0.18
<i>Cotesia rubecula</i> ^{d,f,j}	4.89 \pm 0.88a	6.54 \pm 1.08a	8.78 \pm 1.82b	2,15	4.62	0.03
<i>Diadegma insulare</i> ^d	0.59 \pm 0.06	0.84 \pm 0.16	0.76 \pm 0.16	2,21	0.20	0.82
Chalcidoidea ^{d,k}	51.60 \pm 4.53	45.44 \pm 2.03	46.11 \pm 2.28	2,24	0.88	0.42

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

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

^c Abundance determined from visual abundance per plot.

^d Abundance determined from sticky trap abundance per plot.

^e Abundance determined from pitfall trap abundance per plot.

^f Abundance determined using model with weed height as a covariate.

^g Abundance determined using model with weed diversity as covariate.

^h Abundance determined using model with marketable cabbage yield as a covariate.

ⁱ Abundance determined using model with total herbivore abundance as a covariate.

^j Abundance determined using model with imported cabbageworm abundance as a covariate.

^k Abundance determined using model with total predator abundance as a covariate.

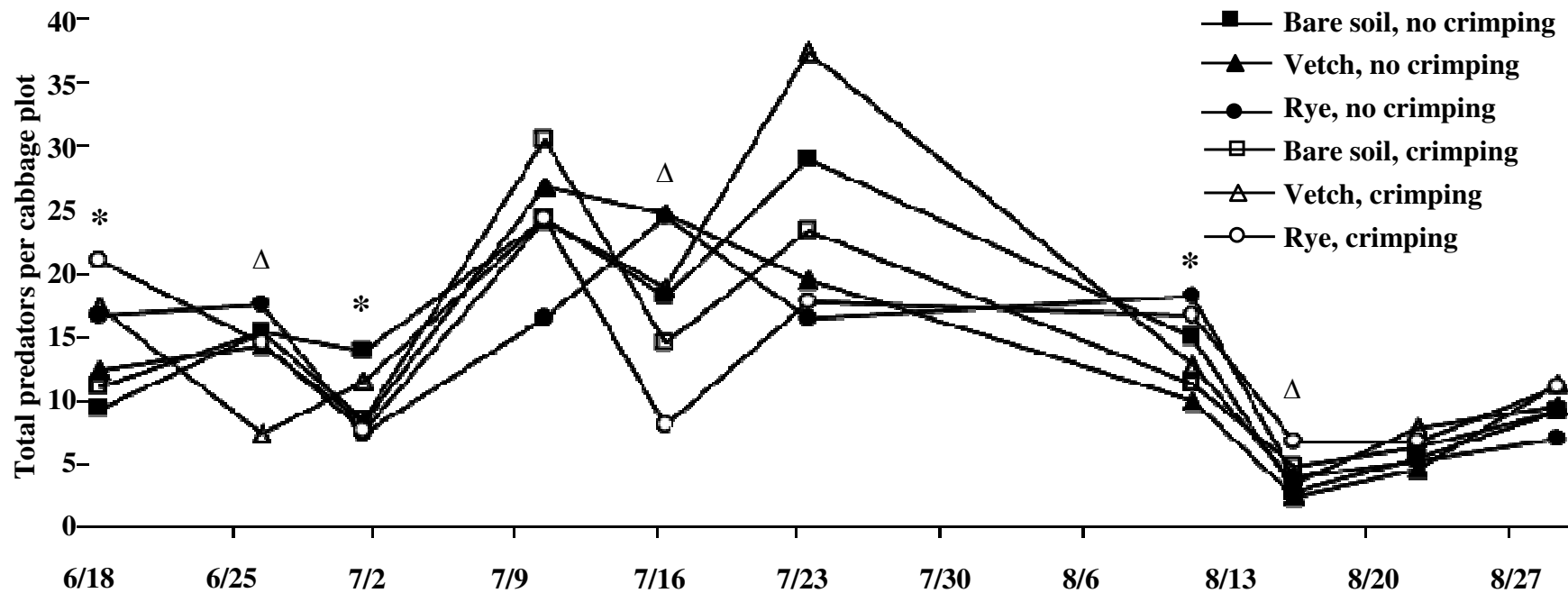


Figure 3.1. Total predator abundance on yellow sticky traps throughout the cabbage growing season in experimental plots with different mulch species (bare soil, rye, vetch) and mulch management treatments (no crimping, crimping). Asterisks and delta symbols above lines indicate significant differences across mulch species and management, respectively according to LSMeans ($\alpha= 0.5$).

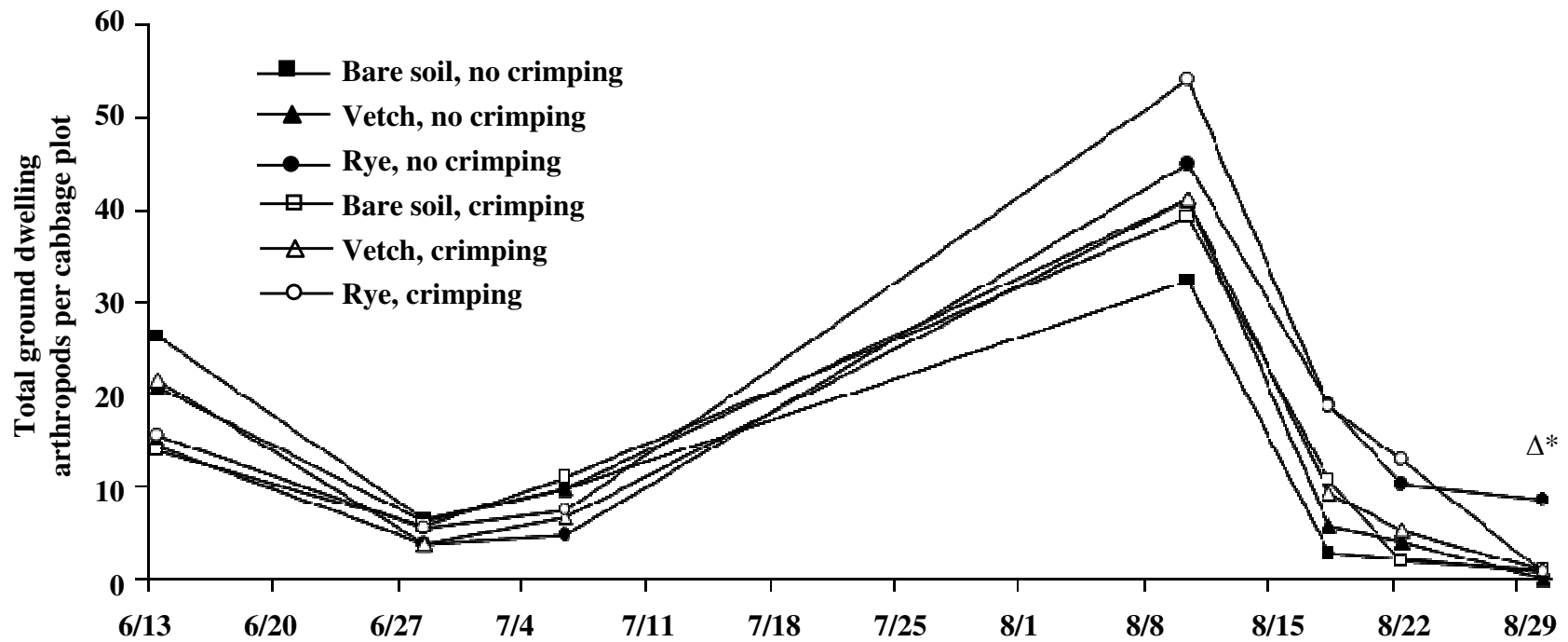


Figure 3.2. Total ground dwelling predators throughout the cabbage growing season in experimental plots with different mulch species (bare soil, rye, vetch) and mulch management treatments (no crimping, crimping). Asterisks and delta symbols above lines indicate significant differences across mulch species and management, respectively according to LSMeans ($\alpha=0.5$).

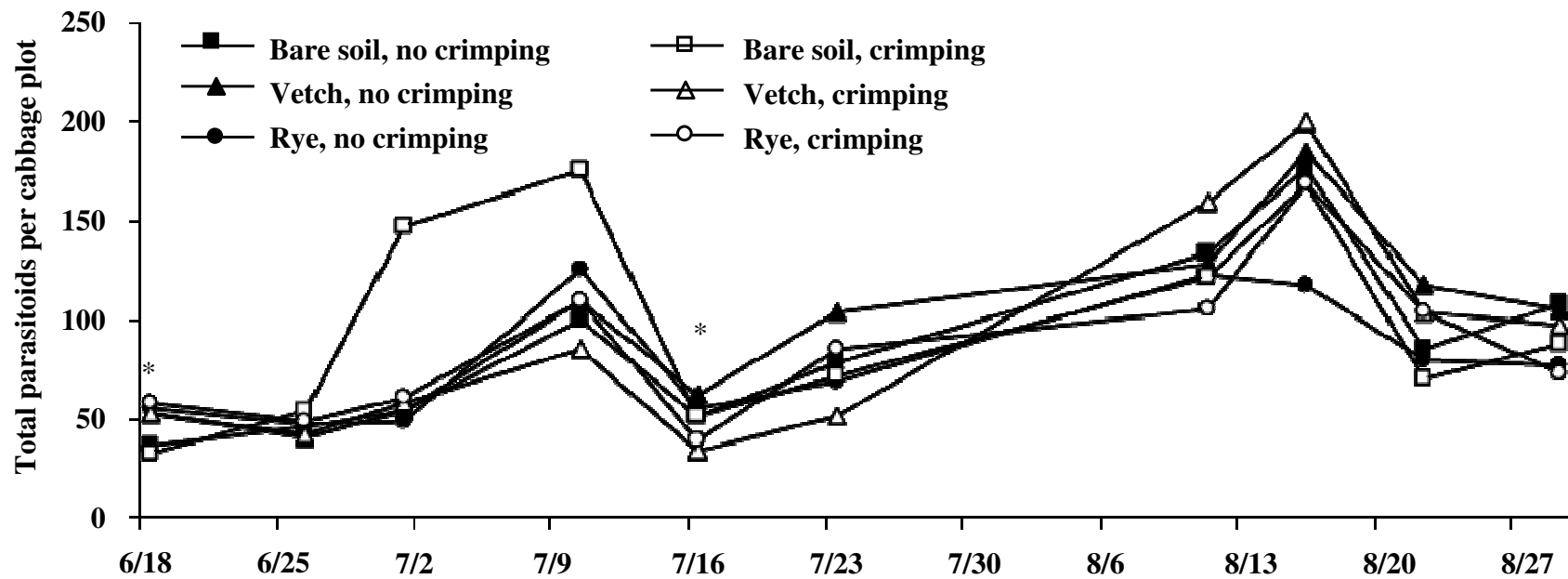


Figure 3.3. Total parasitoid abundance on yellow sticky traps throughout the cabbage growing season in experimental plots with different mulch species (bare soil, rye, vetch) and mulch management treatments (no crimping, crimping). Asterisks above lines indicate significant differences across mulch species according to LSMeans ($\alpha = 0.5$).

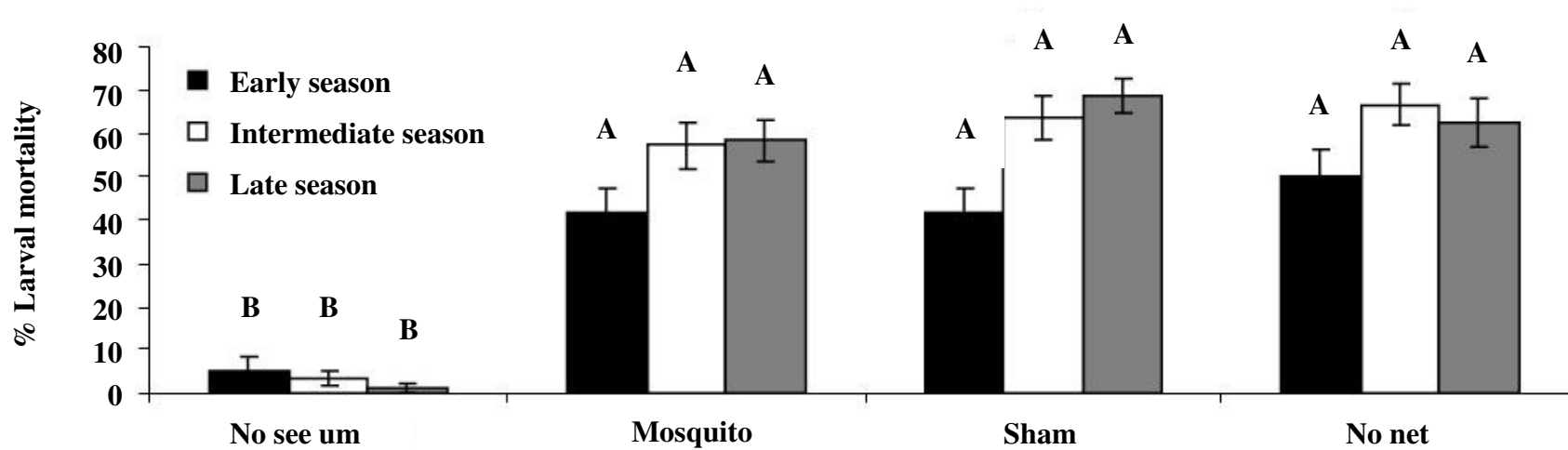


Figure 3.4. Percent larval mortality (Mean \pm SEM) of the imported cabbageworm across natural enemy exclusion cages. Letters above bars indicate significant differences according to LSMeans ($\alpha = 0.5$).

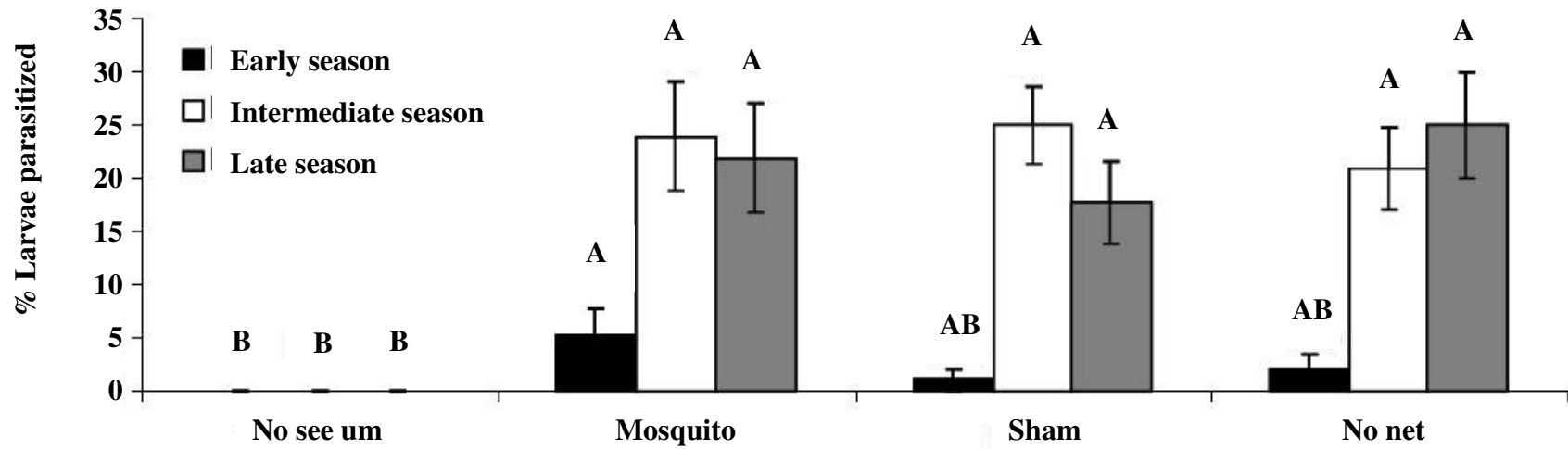


Figure 3.5. Percent of imported cabbageworm larvae parasitized (Mean \pm SEM) across natural enemy exclusion cages. Letters above bars indicate significant differences according to LSMeans ($\alpha = 0.5$).

Discussion

Mulch, weed, and cabbage yield measurements. Mulch species and management or row-middles created habitats within the cabbage field with distinct structural complexity and vegetational complexity (e.g. weed community). For example, mulch management changed the height of the mulch in the row middles, with crimping reducing mulch height during the early and intermediate portion of the growing season (Table 3.1). On the other hand, different mulch species resulted in different amounts of biomass present in the row middle with rye plots containing the greatest amount of structure. Hairy vetch mulch decayed quicker than rye mulch, leading to less structure in the row middles. These plots resembled bare soil plots late in the growing season. Additionally, rye mulch successfully suppressed weed height, abundance, and richness compared to bare soil plots (Table 3.3). This supports past observations in vegetable crops by Liebman and Dyck (1993) and Teasdale (1998).

The presence of rye mulch reduced marketable cabbage yield and led to greater non-marketable yield (Table 3.4). Negative effects of rye on cabbage yield have been observed in the past and may be the result of rye's allelopathic effects, light competition, or tie-up of nitrogen from slow decaying rye (Schonbeck et al. 1993). It is suggested that killing the rye cover crop earlier in the season or reducing the density of the cover crop may reduce these effects and maintain cabbage yields comparable to non-mulched plots (Mochizuki et al. 2008). It should also be noted that no nitrogen sidedress application was made, so nitrogen was likely limiting, especially in rye treatments.

Arthropod communities. The response of mobile predators sampled on sticky traps was inconsistent during the growing season. Total predator abundance responded negatively to

mulching during the early portion of the cabbage growing season and total predator abundance was greater in mulched plots later in the season (Figure 3.1). Mulch management also appeared to have a mixed effect on total predator abundance. When considering abundance of ground dwelling predators, ground cover had little effect on total predator abundance (Figure 3.2). However, on the last sampling date, ground dwelling predators appeared to prefer rye plots without crimping.

Positive responses of predators to mulching have been observed in potatoes, peppers, and collards (Johnson et al. 2004, Pullaro et al. 2006). In these cases, mulching may create habitats that provide additional food sources (e.g. detritivore prey) and protection (Langellotto and Denno 2004). In addition to this study, negative responses of predators to mulching have also been observed in crops such as potatoes and turnips (Wiedenmann et al. 2004, Manrique et al. 2010). Complex habitats may serve to interfere with visual and chemical cues (e.g. Finch and Collier 2000, Randkofer et al. 2010).

During the early cabbage growing season, parasitoid abundance was positively impacted by the presence of rye mulch (Figure 3.3). However, parasitoid populations and parasitism rates of the imported cabbageworm (Figure 3.5) are minimal during the early season and therefore may have a limited impact on pest suppression.

Arthropod abundance. Mulch management and species had an impact on two pests: the striped flea beetle and the imported cabbageworm (Table 3.5). In the past, vegetational complexity provided by *Brassica* weed species in collard plots had an impact on flea beetle populations (Schellhorn and Sork 1997), with more flea beetles present in plots with weed polycultures than bare soil. This study found structural complexity to influence flea beetle populations. In

particular, striped flea beetles were slightly more abundant in standing rye mulched cabbage plots compared to crimped plots. It appears that the height of the mulch did not interfere with pest movement or host finding into plots with standing rye, although the height of surrounding companion plants has demonstrated an interference effect in the past with another *Brassica* pest, the cabbage root fly (Finch et al. 2003).

The imported cabbageworm responded to mulch species, with greater abundance in plots with rye mulch compared to bare soil or vetch plots. This is contrary to past observations of the imported cabbageworm, in which populations were lower in cabbage with rye mulch than non mulched plots (Bottenberg et al. 1997). Banks (1998) has attributed any difference in imported cabbageworm abundance across habitats of varying complexity with differences in predation. He suspected that the imported cabbageworm was unresponsive to within field complexity due to the high mobility, flight patterns, and widespread oviposition patterns of the imported cabbageworm. Instead, the greater structure in the row middle may provide shelter and greater protection from predators.

Mulch management and species impacted the abundance of several natural enemies (Table 3.6). The presence of rye mulch was associated with lower populations of the pink lady beetle and *Poecilus sp.* ground beetle. For the pink lady beetle, these results are contrary to the findings of Szendrei and Weber (2009), who observed greater abundance of the pink lady beetle in mulched potatoes compared to control potato plots. Reduced predator populations suggest a reduced encounter rate and hunting efficiency of predators in complex agricultural environments (Legrand and Barbosa 2003).

This study found a positive impact of rye mulch on the abundance of the generalist predators: *Harpalus pennsylvanicus*, *Pterostichus permundus*, and Linyphiidae spiders (Table

3.8). Contrary to these results, Wiedenmann et al. (2004) found no impact of mulching on the abundance of ground beetle species when comparing mulched and non-mulched garden plots. Additionally, a review by Sunderland and Samu (2000) reported that in previous studies, mulching had no effect on Linyphiid spider abundance compared to other forms of habitat management.

Several mechanisms may explain these positive responses of generalist predator abundance to habitat complexity. Elton (1958) first proposed the enemies hypothesis, suggesting complex habitats would enhance predation of pests in cabbage. Complex habitats may provide protection, further resources, ideal microclimates, or alternative prey such as detritivores which may support greater natural enemy populations (Root 1973, Landis et al. 2000, Sunderland and Samu 2000). These complex habitats may also increase the availability of prey or hosts, or enhance the efficiency of natural enemies. Complex habitats may reduce negative interactions between predators, including intraguild predation such as cannibalism, allowing greater pest suppression (Finke and Denno 2002, Finke and Denno 2006).

The specialist parasitoid *Cotesia rubecula*, was significantly more abundant in rye mulched plots (Table 3.8). Vegetational complexity has influenced *C. rubecula* abundance in the past with higher populations in broccoli with interplanted flowers (Zhao et al. 1992). The impact of structural complexity on *C. rubecula* provided by rye and vetch mulch has not been reported in current literature. *Cotesia rubecula* species relies on specific odor cues from the feeding damage of its host, the imported cabbageworm. The parasitoid will preferentially land on and search plants with imported cabbageworm feeding damage (Agelopoulos and Keller 1994b). However, it is important to note that mulching did not interfere with these signals.

Significant covariates for herbivores. Weed height or diversity impacted the abundance of every major herbivore. This supports results from 2010 and 2011, in which weed pressures influenced herbivore abundance. I suspect that weeds provide shelter, alternative resources, and attractive microclimates for these pest species. In general, total predator abundance also impacted abundance of the imported cabbageworm, diamondback moth, and cabbage looper, suggesting efficiency of predators and predation may be influencing herbivore populations in the field.

Significant covariates for natural enemies. Weed height or diversity also impacted natural enemy abundance for eight major natural enemies. The relationships between weeds and arthropod abundance in *Brassica* crops has been demonstrated in the past, including the role of weed height (Finch et al. 2003) and weed diversity (Andow 1988, Schellhorn and Sork 1997, Broad et al. 2008). The weeds in the row-middle may be providing shelter, resources, alternative prey. Alternatively, weeds may reduce time spent hunting on cabbage plants or influence hunting efficiency leading to changes in natural enemy abundance. Marketable cabbage yield had a limited impact on predators, with a single ground beetle responding negatively to marketable cabbage yield. In this case, *Cyclotrachelus sodalists* may find hunting and movement easier on smaller cabbage plants. Although the generalist predators in this study did not appear to be influenced by prey abundance, host abundance influenced *C. rubecula* and Chalcidoidea abundance. As in 2010 and 2011 (see Chapter 2), *Cotesia rubecula* and the hyperparasitoids included in this study appear to be following their hosts and potentially the stronger host odor signals in mulched plots. Total predator abundance significantly impacted multiple ground dwelling arthropods. For the predators negatively impacted by predator abundance (e.g. *Poecilus* sp.), intraguild predation may be impacting species abundance.

Natural enemy exclusion cages. Mortality and parasitism rates in the cabbage field were not impacted by mulch management or species. Similar results have been observed in potatoes, in which mulching had no impact on predation rates (Szendrei et al. 2010). Although natural enemy abundance was greater in rye mulch plots, the presence of cover crop mulch may interfere with the mobility of predators searching for prey, reducing the efficiency of predators (Legrand and Barbosa 2003, Tylianakis and Romo 2010). Complex habitats may interfere with visual (Ferran and Dixon 1993) or chemical (Randlkofer et al. 2010) searching cues used by natural enemies, leading to lower capture and consumption rates. Intraguild predation, including cannibalism, may also be greater in complex habitats with higher predator populations (Tylianakis and Romo 2010).

The results from the natural enemy exclusion cages highlight the importance of small predators in cabbage pest management. At each sampling date, the guild of small predators was responsible for the majority of predation within the cages. In other studies, larger natural enemies (e.g. lady beetle adults, large ground beetles, etc.) are often surveyed and examined for their pest suppression in cabbage (e.g. Grevstad and Klepetka 1992, Armstrong and McKinlay 1997), while the guild of small natural enemies is overlooked. Natural enemies such as syrphid fly larvae, lacewing larvae, coccinellid larvae, minute pirate bugs, and Linyphiid spiders which were observed feeding on prey inside the exclusion cages, have provided biological control in past studies (Eigenbrode et al. 1996, Schmaedick and Shelton 2000, Reddy et al. 2004). Many of these natural enemies have demonstrated an ability to readily consume cabbage pests and search waxy leaf surfaces that larger predators such as coccinellid adults, Lycosids, and Phalangiids cannot access (Eigenbrode et al. 1996, Schmaedick and Shelton 2000, Reddy et al. 2004). Future

research in conservation biological control with cabbage should examine practices that enhance this guild of small predators.

Summary. Mulch management and species had no impact on most pest species. The presence of mulch had mixed effects on natural enemies, although several ground beetles and Linyphiid spiders were positively impacted by mulching. The guild of small predators including these Linyphiid spiders, appear to be responsible for most predation in the field.

In addition to the direct effects of the mulching (Figure 1.3), possible indirect effects of mulching (Figure 1.4) were considered through the examination of covariates such as marketable cabbage yield, herbivore abundance, and natural enemy abundance. Although the exact mechanisms for the trends observed in arthropod abundance are unknown, it appears that both direct and indirect factors are influencing arthropod populations, particularly weed height and diversity.

It is possible that habitat structure at a larger spatial scale would have had a larger impact on insect abundance and biological control. At larger spatial scales, trap cropping, floral borders, and diversity at the landscape level have been shown to impact natural enemy abundance (e.g. Mitchell et al. 1997, Mitchell et al. 2000, Hooks and Johnson 2003, Lee and Heimpel 2005, Jonsson et al. 2012). On a smaller scale, changes in leaf surface composition (Eigenbrode et al. 1996) and plant architecture (Gingras et al. 2003) can also modify natural enemy and pest abundance, although this was not examined in my study.

Although a diverse community of pests attack cabbage, it is necessary to examine the impact of mulching on predation and parasitism of other pests, particularly other lepidopteran pests causing significant damage in Michigan cabbage. Future studies should focus on mulching

practices that maintain cabbage yields while enhancing predation and parasitism of several cabbage pests. The mechanisms behind the trends observed in this study are still unclear. In particular, future work should determine whether visual or odor cues are involved in the habitat preferences of those natural enemies that were positively influenced by the presence of mulches.

Ch. 4

The role of olfactory cues from cover crop mulch on two generalist and one specialist natural enemy in cabbage

Introduction. The imported cabbageworm *Pieris rapae* L. (Lepidoptera: Pieridae) is considered one of the greatest foliar cabbage pest in the United States (Schmaedick and Shelton 1999, Wold-Burkness et al. 2005). In Michigan, this pest is often one of the first butterflies to appear in the spring and last butterflies observed in the fall. The presence of this pest throughout the cabbage growing season, its high fecundity, and its high mobility (e.g. Richards 1940), have led the imported cabbageworm to become a serious threat to both early and late season cabbage production in Michigan.

Natural enemies can provide significant control of the imported cabbageworm in cabbage fields. Schmaedick and Shelton (1999) observed up to 80% egg and larval mortality due to natural enemies. Lady beetles (Coleoptera: Coccinellidae), predatory stink bugs (Hemiptera: Pentatomidae), spiders (Araneae), and ground beetles (Coleoptera: Carabidae) are among the generalist predators feeding on the imported cabbageworm (Schellhorn and Sork 1997, Schmaedick and Shelton 2000, Suenaga and Hamamura 2001, Moreno et al. 2010). Specialist natural enemies such as the parasitoid *Cotesia rubecula* Marshall (Hymenoptera: Braconidae), provide additional pest suppression. In Michigan, parasitism rates of the imported cabbageworm by *C. rubecula* have recently been observed up to 71% (Herlihy et al. 2012).

Through the manipulation of the habitat within a cabbage field, these natural enemies may be conserved, enhancing the pest management services they provide. Past studies have observed habitats with greater structural complexity to support greater natural enemy populations.

Although enhancement of natural enemy populations has been observed through habitat management in a variety of crops (Landis et al. 2000), it is unclear how different forms of structural complexity due to mulching may influence the natural enemy community in cabbage. Xu et al. (2011) observed greater natural enemy populations in the presence of mulch. However, the response and strength of arthropod responses may vary with different types of mulching practices.

For arthropods that respond positively to mulching, structurally complex habitats may provide alternative prey, enhance efficiency of predators, and provide protection from intraguild predators (Langellotto and Denno 2004). It is also suspected that structurally complex habitats influence the visual and chemical cues that natural enemies rely on when searching for prey and hosts in cabbage (e.g. Finch and Collier 2000, Randkofer et al. 2010). Chemical cues appear to play a particularly important role in attraction of natural enemies to the habitat and ability of the natural enemy to locate herbivores within a cabbage field.

Feeding damage and frass from *Pieris rapae* larvae release a blend of volatiles into the surrounding environment (Agelopoulos and Keller 1994c, Mumm et al. 2008). These “resource-indicating odors” indicate the presence of *P. rapae* and have influenced the behavior of natural enemies in the past (Schroeder and Hilker 2008). Generalist predators, such as the spined soldier bug, *Podisus maculiventris* (Hemiptera: Pentatomidae), have demonstrated less discrimination of odor cues than specialist natural enemies. The responsiveness of generalist predators to damaged cabbage may be limited by cabbage cultivar and environmental conditions (Vuorinen et al. 2004). Generalists may also respond to a variety of resource-indicating odors from multiple herbivores or they may not rely primarily on olfactory cues to find herbivores (Rossbach et al. 2005).

On the other hand, the specialist *Cotesia rubecula* has demonstrated consistent attraction to the odors from cabbage damaged by caterpillars, including the diamondback moth and the imported cabbageworm (van Poecke et al. 2003). *Cotesia rubecula* is also highly attracted to the frass of imported cabbageworm larvae (Agelopoulos and Keller 1994a). The presence of these volatiles resulting from larval feeding lead *C. rubecula* to land on infested cabbage plants and increases the parasitoid's time spent searching for its host (Agelopoulos and Keller 1994b). This suggests *C. rubecula* relies on relatively specific odor cues from lepidopteran damage compared to generalist predators in cabbage.

Complex habitats create a greater diversity of background odors in the environment. This complex blend of odors accompanies the more specific cues from the herbivores that indicate their presence. Schroeder and Hilker (2008) have found background odors to be either: 1) irrelevant to the natural enemy's ability to find herbivores 2) interfere with the natural enemy's ability to find herbivores due to masking of the resource-indicating odor or 3) enhance a natural enemy's ability to find herbivores. It is unknown how background odors from decaying cover crop mulches influence natural enemies. However, it is possible that discrimination of odors from different mulching treatments may also vary between generalist and specialist natural enemies.

In this study, I examined the effects of mulch species and management on arthropod behavior. I observed the role of odor cues from mulch on habitat choices of two generalist predators (spined soldier bug and convergent lady beetle) and one specialist parasitoid (*Cotesia rubecula*).

Materials and Methods

Y-tube olfactometer

Insects. Imported cabbageworm larvae were reared at Michigan State University in a greenhouse colony. Imported cabbageworm originated from the MSU Horticulture Farm (East Lansing, MI) and maintained for c.a. 10 generations. Insects were kept in 47.5 x 47.5 x 93 cm mesh bug dorm cages (Megaview Science Co., Ltd., Taichung, Taiwan) with a 16:8h L:D cycle at 23-28°C. Larvae were reared on Brussels sprouts (*Brassica oleracea* var. “Churchill”; Johnny’s Selected Seeds, Albion, ME) *ad libitum* and adults were fed a 10% honey solution upon emergence (Pure Clover Honey, Meijer Distribution Inc., Lansing, MI).

Third instar spined soldier bugs were provided by T.A. Coudron (Biological Control of Insects Research Laboratory, USDA-Agricultural Research Service, Columbia MO). For rearing conditions and diet of spined soldier bugs, see Coudron et al. (2012). These predators were used for assays upon arrival.

Adult convergent lady beetles were purchased from Rincon-Vitova Insectaries (Ventura, CA). Beetles were placed in petri dishes (150 x 15 mm; VWR, Radnor, PA) and fed a 10% honey solution upon arrival. Convergent lady beetles were held at 10°C until needed for assays. Convergent lady beetles were removed from the fridge 24 h prior to the start of an assay and kept in the laboratory at 25°C. To eliminate any effects that the sex of the parasitoid may have on odor preference, only female beetles were used in subsequent assays.

Cotesia rubecula were reared in a greenhouse colony at Michigan State University. *Cotesia rubecula* were originally collected from the MSU Horticulture Farm in summer 2012 and maintained c.a. 6 generations. Parasitoids were reared on imported cabbageworm from the

greenhouse colony previously described. Adult wasps were fed a 10% honey solution *ad libitum* upon emergence. Due to the unresponsiveness of naïve parasitoids, adult parasitoids were exposed to first and second instar imported cabbageworm for 24 h prior to use in y-tube assays. Only female wasps were used in assays.

Odor sources. Odor sources included clean air, mulch (vetch, rye, or both vetch and rye), damaged cabbage, and damaged cabbage with different mulches (vetch, rye, or vetch and rye). Among these odor sources, ten treatments were tested within the y-tube olfactometer (see Table 4.1 for list of treatments).

Each odor source consisted of an outer pot (14cm diameter x 12cm height) with a smaller inner pot (8cm x 9cm) placed inside (Figure 4.1). The tops of the two pots were flush with one another. Both pots were filled with plant medium (Sure-Mix Perlite, Michigan Grower Products, Galesburg, MI). For the clean air odor source, both the inner and outer pot was filled with plant medium. For odor sources with damaged cabbage, the inner pot contained three cabbage plants. Cabbage seedlings (*Brassica oleracea* var. “Farao”; Johnny’s Selected Seeds, Albion, ME) were grown for one month (16:8h L:D; 23-28°C) before transplanting three cabbage plants into a 8cm x 9cm pot together. Cabbage plants were grown separately and maintained in separate pots from mulch species to prevent any confounding effects or interactions between mulch and cabbage plants.

For odor sources with mulch, winter rye (*Secale cereale*; Dirt Works, New Haven, VT), hairy vetch (*Vicia villosa*; Johnny’s Selected Seeds, Albion, ME), or both species were planted in the space between the inner and outer pots. Winter rye was planted at a rate of 0.25 ounce/pot. Hairy vetch was planted at a rate of 0.13 ounce/pot. Mulch species were planted at these same

rates for odor sources containing both rye and vetch. After one month, RoundUp was applied to all above ground foliage of cover crop plants and a week later, cover crop mulch was used in bioassays.

Twenty four hours before an assay began, odor sources were placed in individual screen cages (30 x 30 x 30 cm; Bioquip Products, Racho Dominguez, CA). At this time, all inner pots were placed within outer pots. To create herbivore damage on cabbage, six imported cabbageworm at the 5th instar stage were placed on the three cabbage plants in the inner pots and allowed to feed for 24 h.

Table 4.1. List of treatments or choice tests performed for each natural enemy species (spined soldier bug, convergent lady beetle, and *Cotesia rubecula*).

Option 1	Option 2
Air	Damaged cabbage
Air	Vetch mulch
Air	Rye mulch
Air	Vetch and rye mulch
Vetch mulch	Damaged cabbage
Rye mulch	Damaged cabbage
Vetch and rye mulch	Damaged cabbage
Damaged cabbage	Damaged cabbage and vetch mulch
Damaged cabbage	Damaged cabbage and rye mulch
Damaged cabbage	Damaged cabbage and vetch mulch and rye mulch

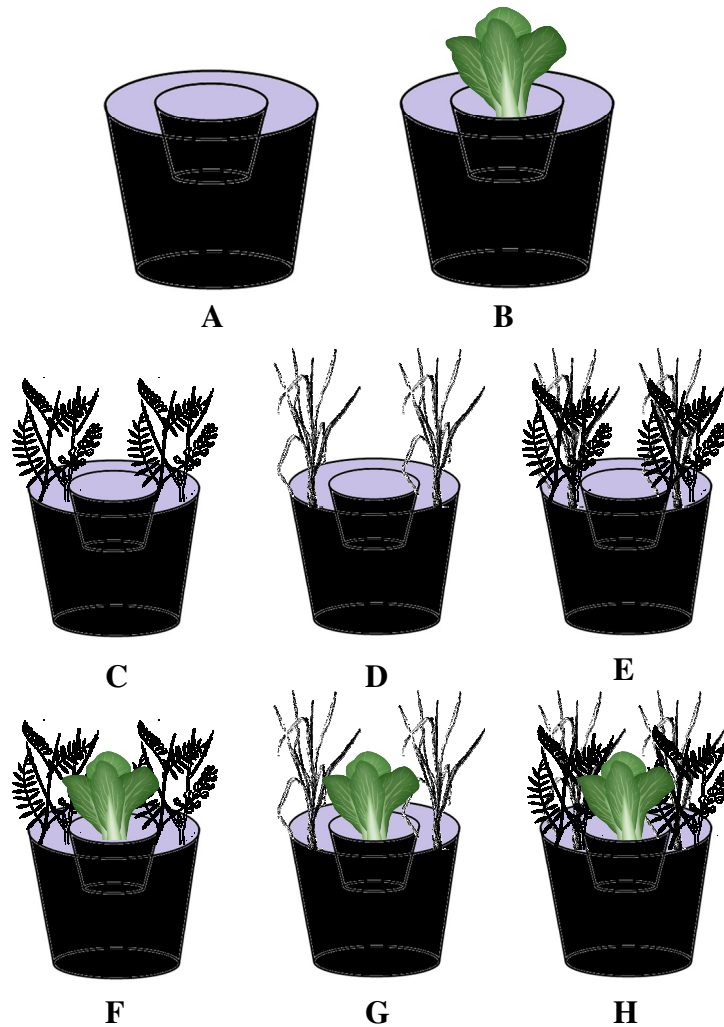


Figure 4.1. Odor sources for y-tube olfactometer. Top row (left to right): clean air (A) and damaged cabbage (B). Second row (left to right): vetch (C), rye (D), and both rye and vetch mulch (E). Bottom row (left to right): cabbage with vetch (F), cabbage with rye (G), and cabbage with both vetch and rye mulch (H).

Y-tube assay. To test olfactory preferences of the spined soldier bug, convergent lady beetle, and *Cotesia rubecula*, a y-tube olfactometer was used (three arms: two 6 cm arms and one 12 cm arm, 2cm diameter, ground glass joints; Michigan State University Glass Blowing Facility, East Lansing, MI). Air filtered through activated charcoal was divided into two streams, each travelling in Teflon tubing leading to two glass chambers (7 L each; Corning Incorporated,

Corning, NY) containing different odor sources and attached to the olfactometer (Analytical Research Systems, Gainesville, FL). Air flow was adjusted for each natural enemy species. Air flow was maintained at 1 L/min for both adult convergent lady beetles and *Cotesia rubecula* adults. However, air flow was reduced for spined soldier bugs and maintained at 0.50 L/min (Vuorinen et al. 2004).

Individual natural enemies were placed at the end of the Y-tube and observed for 15 minutes or until a choice was made. If an insect did not respond within 15 minutes, it was considered nonresponsive. Individual natural enemies were tested once and odor sources were replaced after six insects were assayed. The position of the odor source (left or right chamber) was placed at random and changed between replicates to eliminate positional bias. Between runs, glassware was rinsed with methanol and hexane before drying at 60°C. Each treatment was replicated 28 to 48 times for each natural enemy species.

For each odor source, the number of insects making a choice was analyzed. A G-test with William's correction (Sokal and Rohlf 1995) was performed to test the null hypothesis that the natural enemy had no preference between odor sources.

Results

Y-tube olfactometer. The majority of natural enemies responded in the y-tube, in particular 86% of spined soldier bugs, 95% of convergent lady beetles, and 90% of *C. rubecula* made a choice (Figure 4.2, 4.3, 4.4). However, the three natural enemies tested were not attracted to rye mulch, vetch mulch, or both hairy vetch and rye mulch compared to clean air ($G_{adj} < 3.47$, $df = 1$, $P > 0.06$).

When compared to clean air, the spined soldier bug ($G_{adj} = 0.91$, $df = 1$, $P = 0.34$; Figure 4.2) and the convergent lady beetle ($G_{adj} = 0.58$, $df = 1$, $P = 0.45$; Figure 4.3) did not prefer damaged cabbage. Additionally, the generalist predators were not attracted to damaged cabbage compared to rye mulch, vetch mulch, or both rye and vetch mulch ($G_{adj} < 1.38$, $df = 1$, $P > 0.24$). When damaged cabbage was offered opposite damaged cabbage with different mulch species (e.g. rye, vetch, or rye and vetch mulch), the generalist predators were not repelled or attracted to the presence of mulch ($G_{adj} < 1.47$, $df = 1$, $P > 0.22$).

Contrary to the generalist predators, the specialist natural enemy *C. rubecula* was attracted to damaged cabbage. Significantly more *C. rubecula* chose damaged cabbage over clean air ($G_{adj} = 12.31$, $df = 1$, $P < 0.01$; Figure 4.4). Damaged cabbage was also more attractive to *C. rubecula* than rye mulch ($G_{adj} = 21.05$, $df = 1$, $P < 0.01$), vetch mulch ($G_{adj} = 13.77$, $df = 1$, $P < 0.01$), or both mulch species combined ($G_{adj} = 5.18$, $df = 1$, $P = 0.03$). When the parasitoid was offered damaged cabbage opposite damaged cabbage with different mulch species, it was not affected by damaged cabbage with vetch mulch ($G_{adj} = 0.31$, $df = 1$, $P = 0.58$) or combined rye and vetch mulch ($G_{adj} = 1.27$, $df = 1$, $P = 0.26$). However, it was repelled by damaged cabbage with rye mulch present ($G_{adj} = 10.45$, $df = 1$, $P < 0.01$).

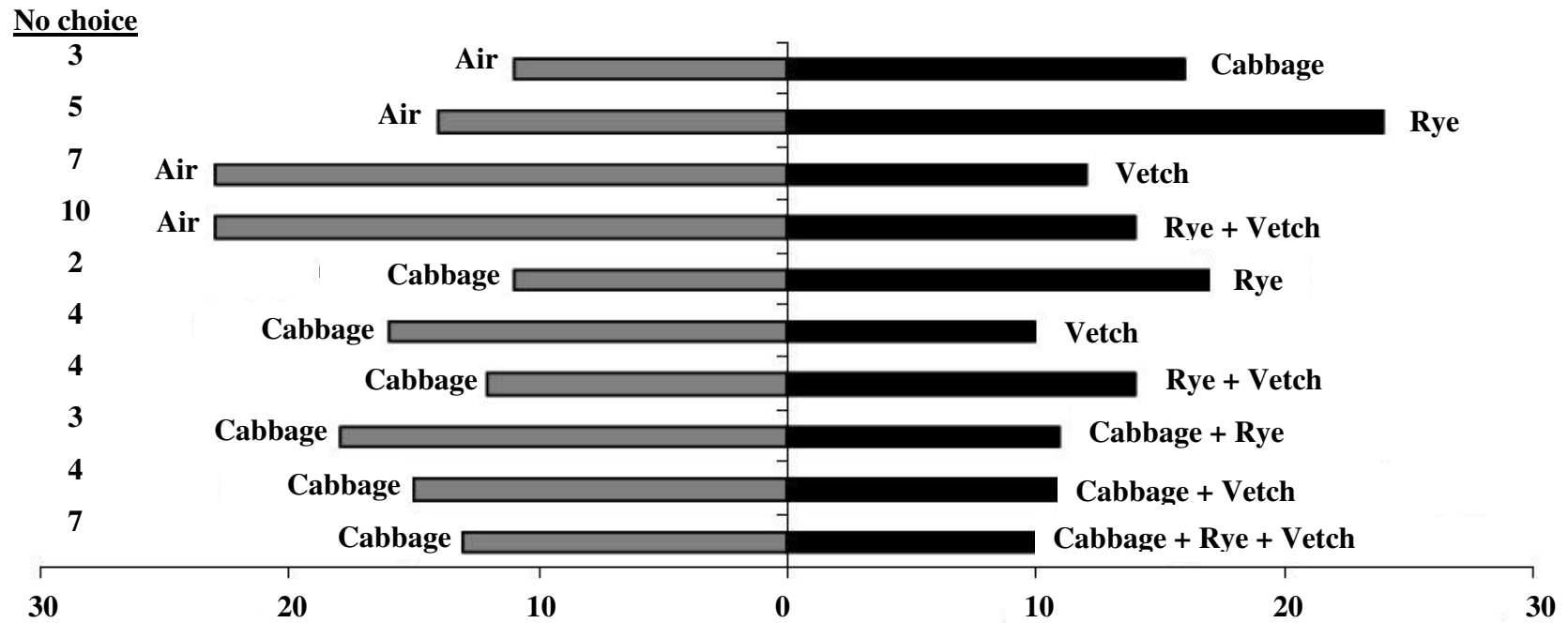


Figure 4.2. Response of spined soldier bug nymphs in Y-tube olfactometer choice test.

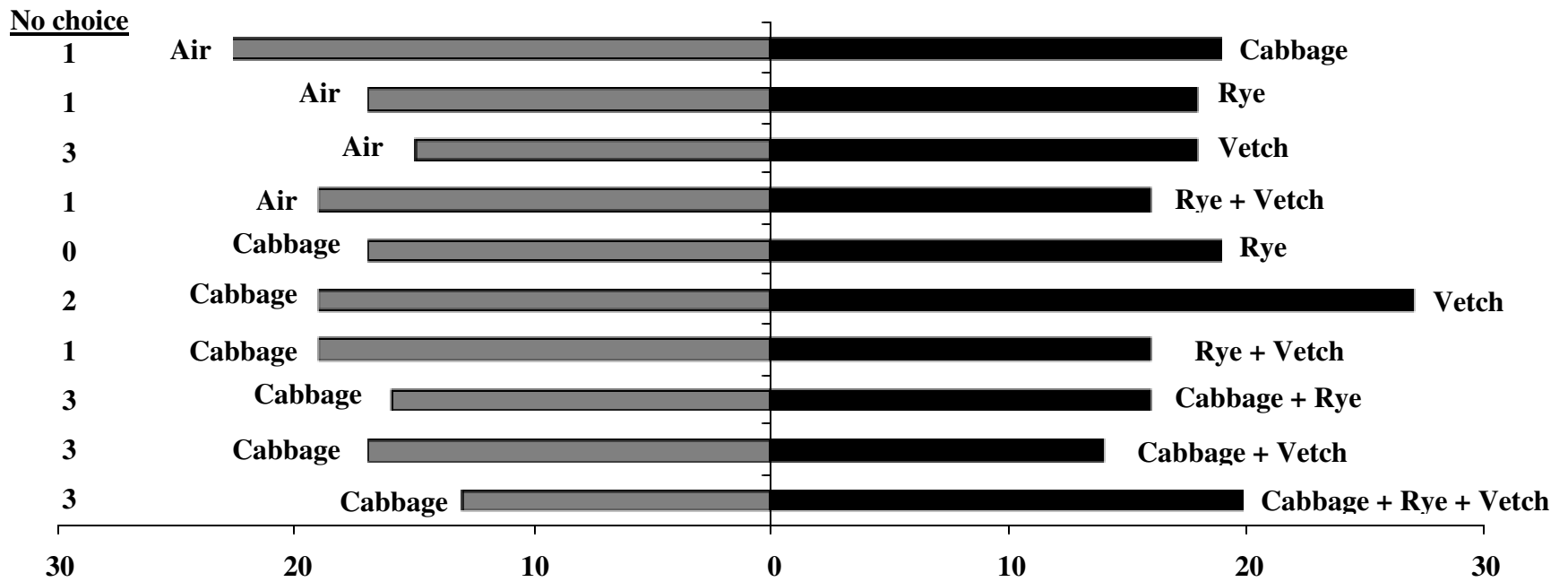


Figure 4.3. Response of convergent lady beetles in Y-tube olfactometer choice test.

No choice

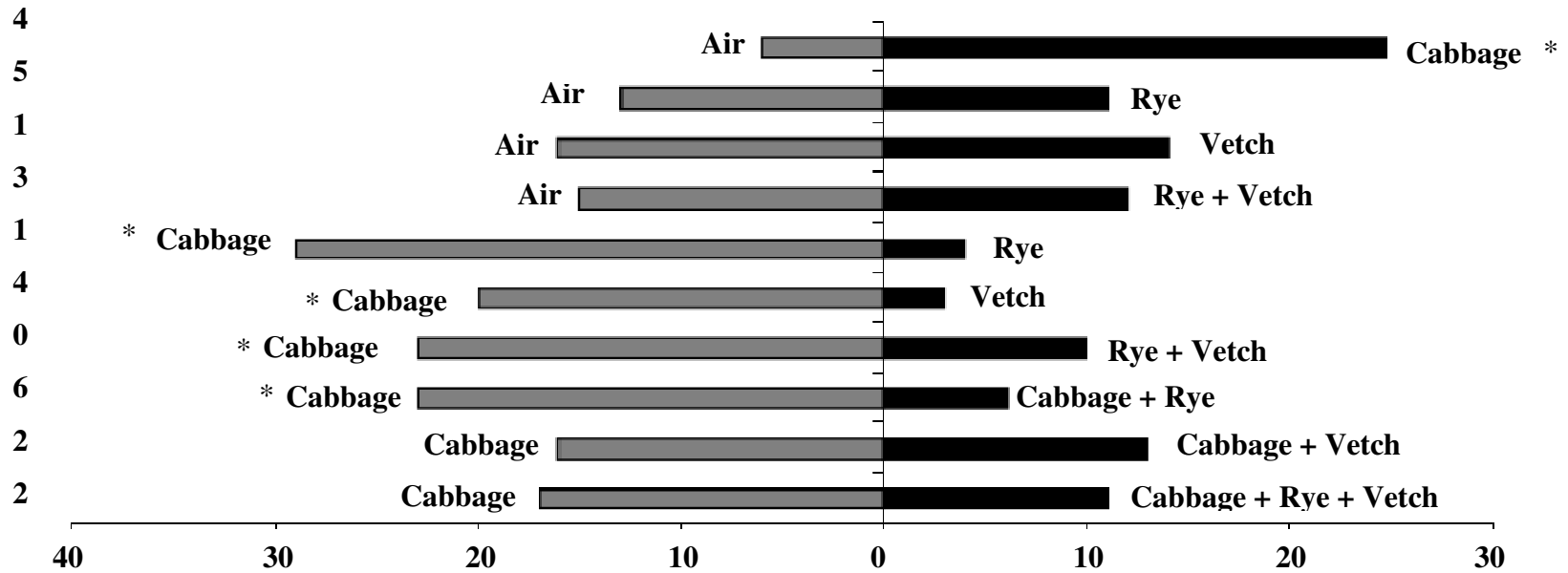


Figure 4.4. Response of *Cotesia rubecula* parasitoids in Y-tube olfactometer choice test. Asterisks indicate significant difference according to *G*-test with William's correction ($\alpha = 0.05$).

Conclusions

Y-tube olfactometer. The choice tests indicated that generalist and specialist natural enemies discriminate odor cues differently when choosing a habitat and searching for an herbivore. Differential responses of generalist and specialist herbivores and natural enemies have been observed in the past and are due to variability of glucosinolate concentrations in *Brassica* cultivars (Giamoustaris and Mithen 1995, Li et al. 2000). Convergent lady beetles and spined soldier bugs were not attracted to damaged cabbage. Although the spined soldier bug and convergent lady beetle have preferred herbivore damaged plants in published studies (Hamilton et al. 1999, Sant'Ana et al. 1999, Acar et al. 2001), this may be due to the inability of these species to discriminate resource-indicating odors with this cabbage cultivar (Vuorinen et al. 2004) or their need for a bouquet of resource-indicating odors from multiple herbivores (Rossbach et al. 2005). These generalist predators may also rely on visual cues rather than odors to detect appropriate habitat and landing sites (Finch and Collier 2000).

On the other hand, *C. rubecula* was highly attracted to resource-indicating odors from damaged cabbage and appears to rely heavily on odor cues for host searching and location. The ability of the imported cabbageworm feeding damage and frass to release attractive volatiles has been well documented for natural enemies such as *C. rubecula* (e.g. Agelopoulos and Keller 1994a, c, van Poecke et al. 2003, Mumm et al. 2008).

The background odors of rye and vetch mulch were neither attractive nor repellent to the generalist natural enemy species tested here; therefore mulch odors appear to be irrelevant background odors in this study. The natural enemies tested may lack receptors to recognize the volatiles from mulch or may become adapted to the mulch odor (Schroeder and Hilker 2008). The lack of mulch odor preference may help to explain the similarity of convergent lady beetle

and spined soldier bug abundance across mulching treatments (see Chapter 3, Table 3.4, 3.6). For the specialist, *C. rubecula*, mulch volatiles do not appear to interfere with the parasitoids preference for damaged cabbage, with the exception of rye mulch. Rye mulch can be considered a masking background odor (Schroeder and Hilker 2008). Rye did not elicit a repellent response from *C. rubecula* when presented alone, however when rye is present with the host plant, it reduced the parasitoids preference for damaged cabbage. Since *C. rubecula* abundance was greater in cabbage field plots with rye mulch (see Chapter 3, Table 3.6), the masking effects of the rye mulch on parasitoid behavior appear to be less important than other factors influencing parasitoid behavior (e.g. intraguild predation, microclimates).

Summary. Mulching does not appear to attract natural enemies and mulching odors are not repellent to generalist predators. However, odors from rye mulch may have masking effects for the specialist parasitoid, *Cotesia rubecula*. Although rye mulch may mask cabbage damage odors, this parasitoid was more abundant in experimental plots with rye mulch (see Chapter 3). Future studies should examine the mechanisms behind the greater presence of *C. rubecula* in mulched plots.

CHAPTER 5.

Conclusions and Future Research

Michigan cabbage production is threatened by a diverse community of insect pests. Habitat management practices that manipulate habitat complexity can conserve natural enemies and enhance biological control, providing improved management of this diverse pest community in cabbage. Enhancing natural enemy populations by habitat management within cabbage fields may reduce grower's reliance on chemical controls, saving them time and money. These practices also lead to greater sustainability and fewer negative impacts on the surrounding environment. This thesis examined the relationship between cabbage arthropods and alternative strategies that manipulate vegetational (living) and structural (non-living) complexity between cabbage rows, in the hopes of providing additional management strategies for Michigan cabbage growers.

In chapter two, I examined habitat management strategies such as reduced weed management intensity and later oat cover crop kill date in strip-tilled cabbage. Greater vegetational complexity from reduced weed management intensity led to reduced abundance of several key cabbage pests. In general, greater vegetational and structural complexity between cabbage rows enhanced populations of generalist natural enemies, including several generalist predators with active hunting strategies. These results suggest reduced weed management and mulch from late killed oats may enhance pest suppression through conservation of natural enemies and could be incorporated into integrated pest management plans. However, before these alternative habitat management strategies can be implemented, further work is needed: ultimately, cabbage yields must be comparable to conventional practices. Future research should

fine-tune weed management and mulching strategies that maintain cabbage yields and do not enhance hyperparasitism.

In chapter three, I examined different mulch species and mulch management. The goal of this chapter was to determine the value of different mulching practices, including the use of different mulch species (e.g. none, rye, vetch) and management (e.g. crimping or no crimping), by examining the response of arthropods to these management methods. In general, mulch management had a limited impact on cabbage pests and natural enemies. Chapter three results suggest managing mulch through crimping or allowing it to remain standing is not promising as a potential habitat management strategy to enhance natural enemies in cabbage. However, the presence of rye mulch in cabbage plots led to greater abundance of several predators and a specialist parasitoid. Rye mulch may have potential as a form of structural complexity that can enhance biological control. Although I observed no impact of mulch species on biological control of the imported cabbageworm, biological control of other cabbage pests may be impacted by the presence of mulch.

Additionally, the use of rye mulch for habitat management should be investigated with other methods of measuring biological control. For instance, molecular gut content analysis methods can reveal the role of individual predators in managing cabbage pests and identify the individual predator species providing the greatest pest suppression. Video surveillance methods also provide insight into predator species feeding in the field and can identify day time and nocturnal predators of sentinel prey. Further research on habitat management strategies in cabbage should focus on the natural enemies identified as having the greatest role in cabbage pest suppression.

Although the work in this thesis has provided information on the impact of living and non-living complexity on arthropods, the mechanisms responsible are still unknown. The positive response of natural enemies to habitat complexity may be due to the presence of resources such as detritivore prey, protection from intraguild predators, and suitable microhabitats. Negative responses of natural enemies to habitat complexity may be due to other mechanisms such as reduced hunting efficiency and greater intraguild predation. If the mechanisms responsible for the trends observed in this thesis are identified, habitat management strategies can be adjusted to maximize the benefits of natural enemy populations in cabbage.

Chapter four of this thesis examined one possible mechanism behind natural enemy behavior in mulched cabbage. In particular, the role of odor cues from decaying mulch on the behavior of three natural enemies. The preference for odors from damaged cabbage, rye mulch, vetch mulch, and combined rye and vetch mulch were observed. The results from chapter four suggest greater discrimination of specialist natural enemies to damaged cabbage compared to generalist natural enemies. On the other hand, the findings in chapter four indicate that odors from decaying mulch or vetch are neither attractive nor repellent to natural enemies and have limited interfering effects. This indicates a minimal role of olfactory cues in the behavior of natural enemies to choose mulched habitats. However, the role of odor cues should be examined in other natural enemies commonly feeding on the imported cabbageworm and other pests before eliminating the role of olfaction. Based on these results, visual cues are suspected to play a major role in habitat choice of generalist natural enemies. The impact of vegetational and structural complexity between crop rows on visual cues for natural enemies has been unexplored to date and is an avenue for future work.

APPENDIX

Appendix 1.1. Supplementary data

Supplementary Table S1. Arthropods were categorized according to feeding functional group, feeding guild, diet breadth, and hunting mode in 2010 and 2011.

Herbivore taxonomic classification	Feeding functional group	Feeding guild	Diet breadth
Acrididae	Herbivore	Chewing	Generalist
Aphrodinae: Cicadellidae	Herbivore	Sucking	Generalist
<i>Brevicoryne brassicae</i> (Linnaeus)	Herbivore	Sucking	Specialist
<i>Ceramica picta</i> (Harris)	Herbivore	Chewing	Generalist
Chrysomelidae	Herbivore	Chewing	Generalist
Curculionidae	Herbivore	Sucking	Generalist
<i>Delia radicum</i> (Meigen)	Herbivore	Chewing	Specialist
<i>Diabrotica undecimpunctata</i> (Howardi)	Herbivore	Chewing	Generalist
Elateridae	Herbivore	Chewing	Generalist
<i>Lygus lineolaris</i> (Palisot de Beauvois)	Herbivore	Sucking	Generalist
<i>Macrosteles fascifrons</i> (Stål)	Herbivore	Sucking	Generalist
Meloidae	Herbivore	Chewing	Generalist
Miridae	Herbivore	Sucking	Generalist
<i>Myzus persicae</i> (Sulzer)	Herbivore	Sucking	Generalist
<i>Phyllotreta cruciferae</i> (Fabricius)	Herbivore	Chewing	Oligophagous
<i>Phyllotreta striolata</i> (Fabricius)	Herbivore	Chewing	Oligophagous
<i>Pieris rapae</i> (Linnaeus)	Herbivore	Chewing	Specialist
<i>Plutella xylostella</i> (Linnaeus)	Herbivore	Chewing	Specialist
Psyllidae	Herbivore	Sucking	Generalist
<i>Spilosoma virginica</i> (Fabricius)	Herbivore	Chewing	Generalist
<i>Thrips tabaci</i> (Lindeman)	Herbivore	Sucking	Generalist
<i>Trichoplusia ni</i> (Hübner)	Herbivore	Chewing	Generalist
Natural enemy taxonomic classification	Feeding functional group	Hunting mode	
<i>Aelothrips sp.</i>	Predator	Active	
Araneidae	Predator	Sit and wait	
Braconidae	Parasitoid	Active	
Cantharidae	Predator	Active	
Carabidae	Predator	Active	
Chalcididae	Parasitoid	Active	
Chalcidoidea	Parasitoid	Active	
Cleridae	Predator	Active	
<i>Coccinella septempunctata</i> (Linnaeus)	Predator	Active	
<i>Coleomegilla maculate</i> (DeGeer)	Predator	Active	
<i>Cotesia rubecula</i> (Marshall)	Parasitoid	Active	
<i>Diadegma insulare</i> (Cresson)	Parasitoid	Active	
Dolichopodidae	Predator	Active	
<i>Harmonia axyridis</i> (Pallas)	Predator	Active	
<i>Hippodamia convergens</i> (Guérin)	Predator	Active	

Supplementary Table S1 (cont'd)

Natural enemy taxonomic classification	Feeding functional group	Hunting mode
Ichneumonidae	Parasitoid	Active
Lampyridae	Predator	Active
Nabidae	Predator	Active
Neuroptera	Predator	Active
<i>Orius sp.</i>	Predator	Active
Phalangidae	Predator	Active
<i>Podisus maculiventris</i> (Say)	Predator	Active
<i>Propylaea quatuordecimpunctata</i> (Linnaeus)	Predator	Active
Pteromalidae	Parasitoid	Active
Salticidae	Predator	Active
Staphylinidae	Predator	Active
Syrphidae	Predator	Active
Tachinidae	Parasitoid	Active
Tetragnathidae	Predator	Sit and wait

Supplementary Table S2. Mean \pm SEM cabbage biomass, leaf area, and number of leaves per plant mid-season in 2010 and 2011.

Main effects	Cabbage biomass (kg) ^a		Cabbage leaf area per plant (cm ²) ^a		Number of cabbage leaves per plant ^a	
	2010	2011	2010	2011	2010	2011
Oat kill date						
Early	0.41 \pm 0.03a	0.38 \pm 0.04	46.44 \pm 2.54a	12.58 \pm 1.24	17.25 \pm 0.55	12.72 \pm 0.28
Intermediate	0.34 \pm 0.04a	0.35 \pm 0.05	39.97 \pm 4.07a	11.68 \pm 1.73	16.56 \pm 1.06	13.16 \pm 0.40
Late	0.25 \pm 0.04b	0.27 \pm 0.07	29.72 \pm 4.38b	9.66 \pm 2.36	15.44 \pm 1.29	12.16 \pm 0.56
Herbicide intensity						
Low	0.35 \pm 0.03	0.37 \pm 0.05	40.35 \pm 3.26	12.65 \pm 1.70	16.29 \pm 0.68	12.85 \pm 0.38
High	0.32 \pm 0.04	0.29 \pm 0.04	37.06 \pm 3.92	9.96 \pm 1.16	16.54 \pm 0.97	12.50 \pm 0.34
Significance	-----P-value-----					
Oat kill date (KD)	<0.01	0.34	<0.01	0.50	0.45	0.31
Herb. intensity (HI)	0.39	0.19	0.36	0.20	0.83	0.50
KD x HI	0.49	0.36	0.52	0.49	0.77	0.63

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

Supplementary Table S3. Mean \pm SEM number of marketable and non-marketable cabbage heads per plot in 2010 and 2011.

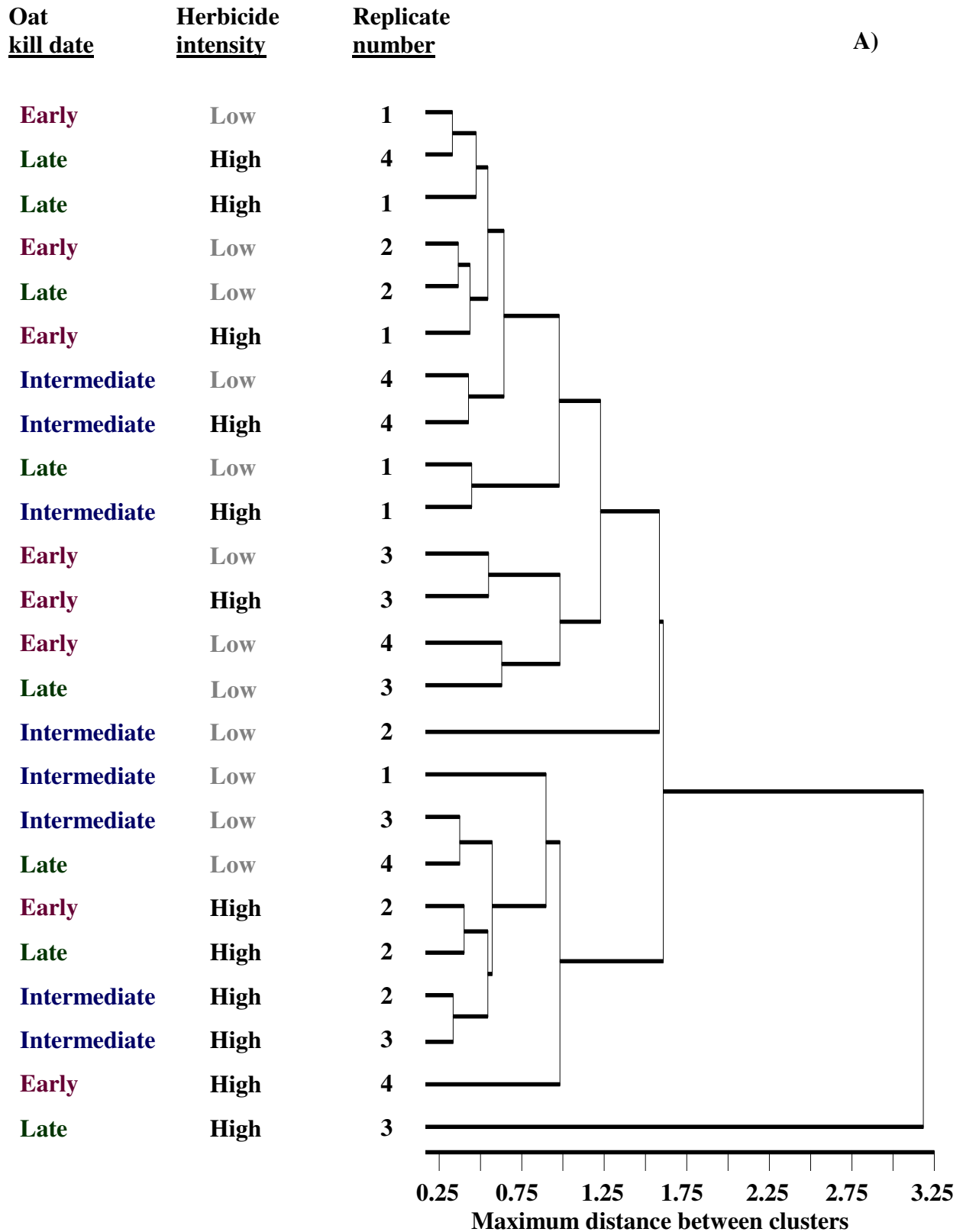
Main effects	Marketable ^a		Non-marketable ^a	
	2010	2011	2010	2011
Oat kill date				
Early	38.63 \pm 0.80a	42.50 \pm 2.09	1.88 \pm 0.67a	5.38 \pm 1.51
Intermediate	34.63 \pm 2.37a	38.88 \pm 3.48	5.88 \pm 2.27a	9.63 \pm 3.67
Late	28.13 \pm 3.45b	36.63 \pm 2.18	12.38 \pm 3.19b	12.25 \pm 2.02
Herbicide intensity				
Low	31.42 \pm 2.78	38.08 \pm 1.99	8.50 \pm 2.63	10.67 \pm 2.06
High	36.17 \pm 1.53	40.58 \pm 2.41	4.92 \pm 1.62	7.50 \pm 2.28
Significance	-----P-value-----			
Oat kill date (KD)	0.01	0.24	<0.01	0.10
Herb. Intensity (HI)	0.08	0.37	0.16	0.22
KD x HI	0.70	0.74	0.78	0.73

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

Supplementary Table S4. Mean \pm SEM number of non-marketable and marketable cabbage heads at harvest in 2012.

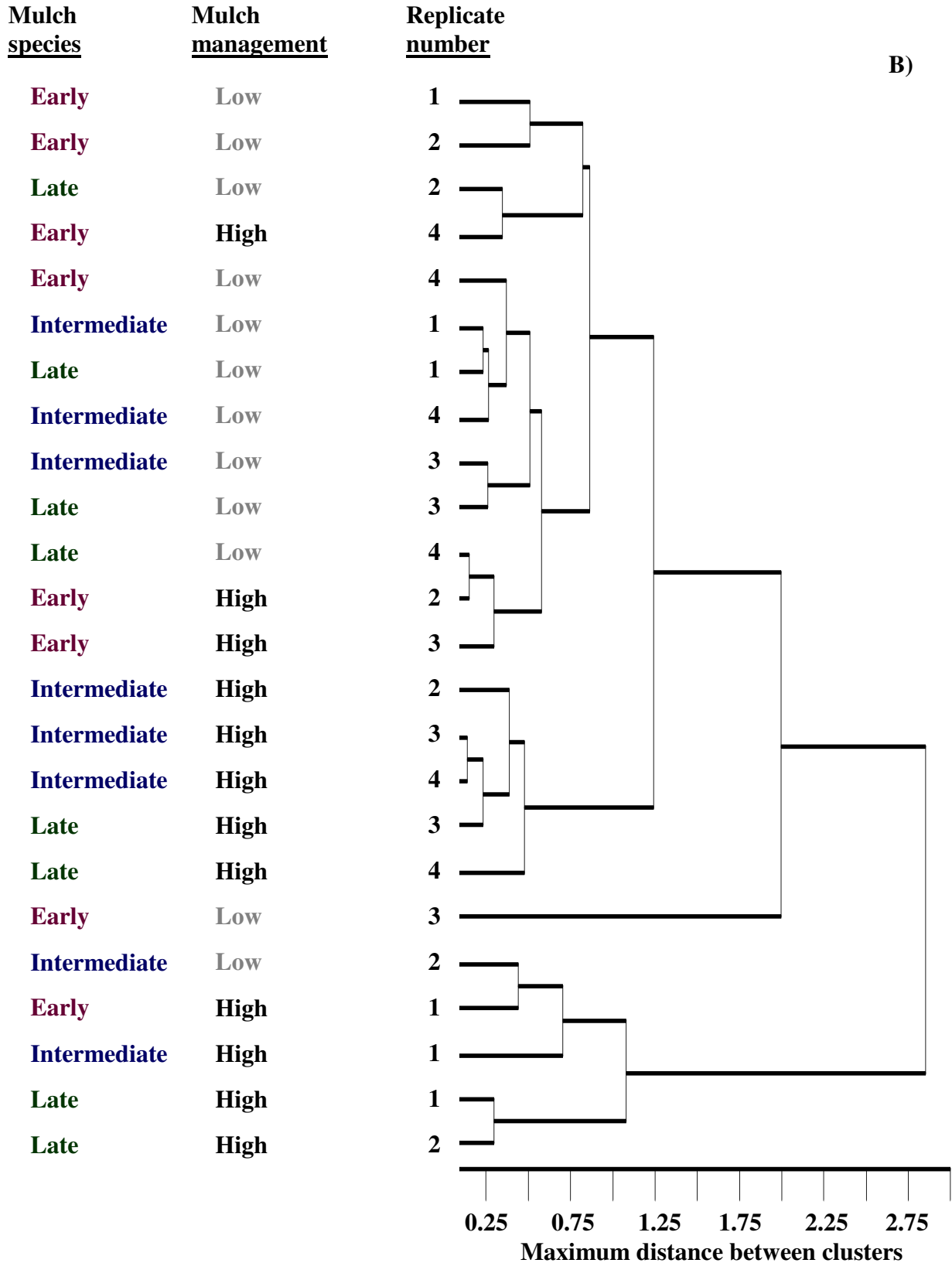
Main effects	Number of Marketable Heads ^a	Number of Non-marketable Heads ^a
Mulch species		
Bare soil	34.00 \pm 4.81a	48.13 \pm 7.44a
Hairy vetch	28.63 \pm 4.11ab	58.38 \pm 4.95ab
Winter rye	16.75 \pm 3.04b	73.75 \pm 4.30b
Mulch management		
No crimping	26.75 \pm 4.03	60.58 \pm 5.67
Crimped	26.17 \pm 3.76	59.58 \pm 5.45
Significance	-----P-value-----	
Mulch species (S)	0.01	0.02
Mulch management (M)	0.64	0.89
S x M	0.07	0.25

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

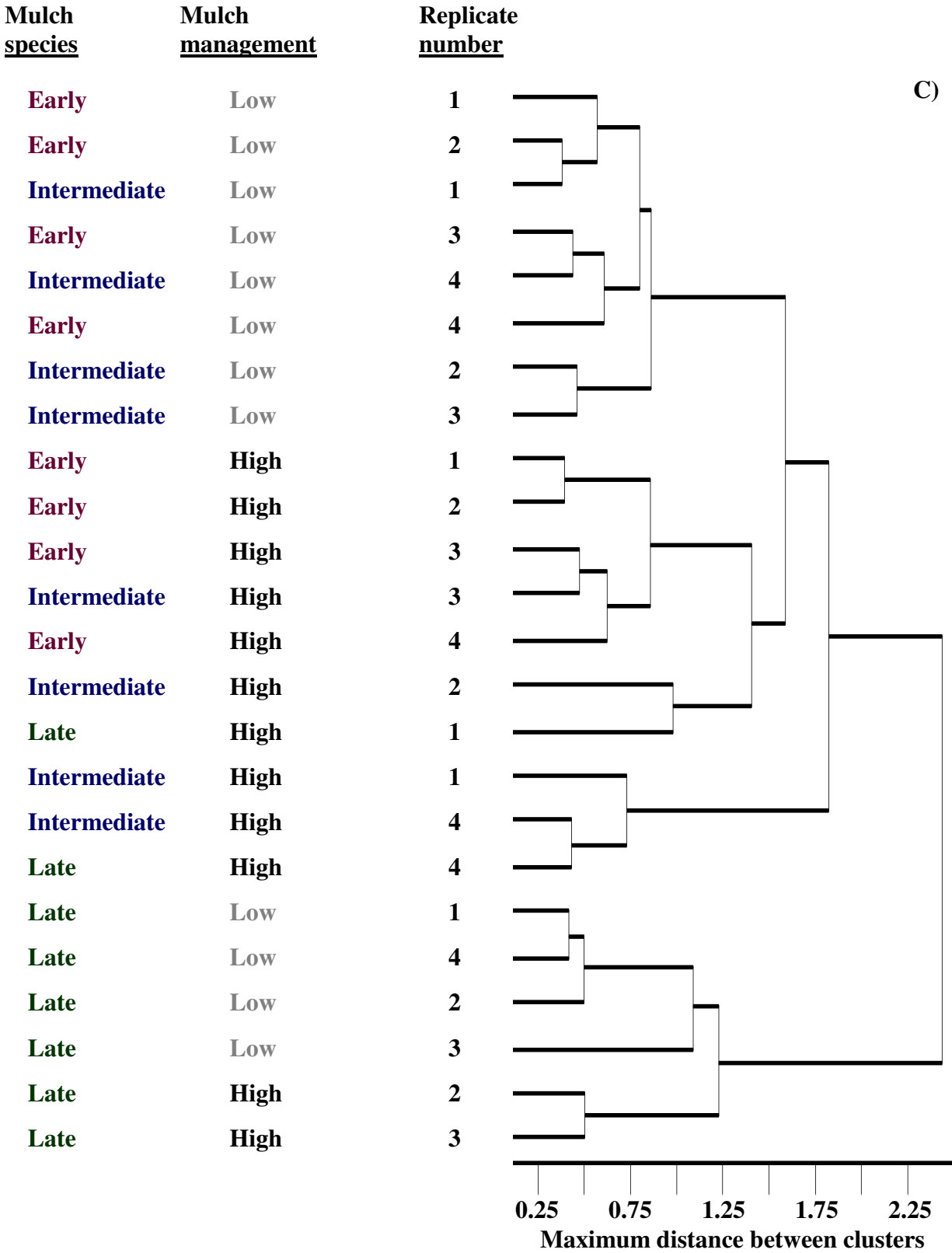


Supplementary Figure S1. Community dendrogram of plots based on average linkage distance for herbivores in 2010 (A) and 2011 (B) and natural enemies in 2010 (C) and 2011 (D).

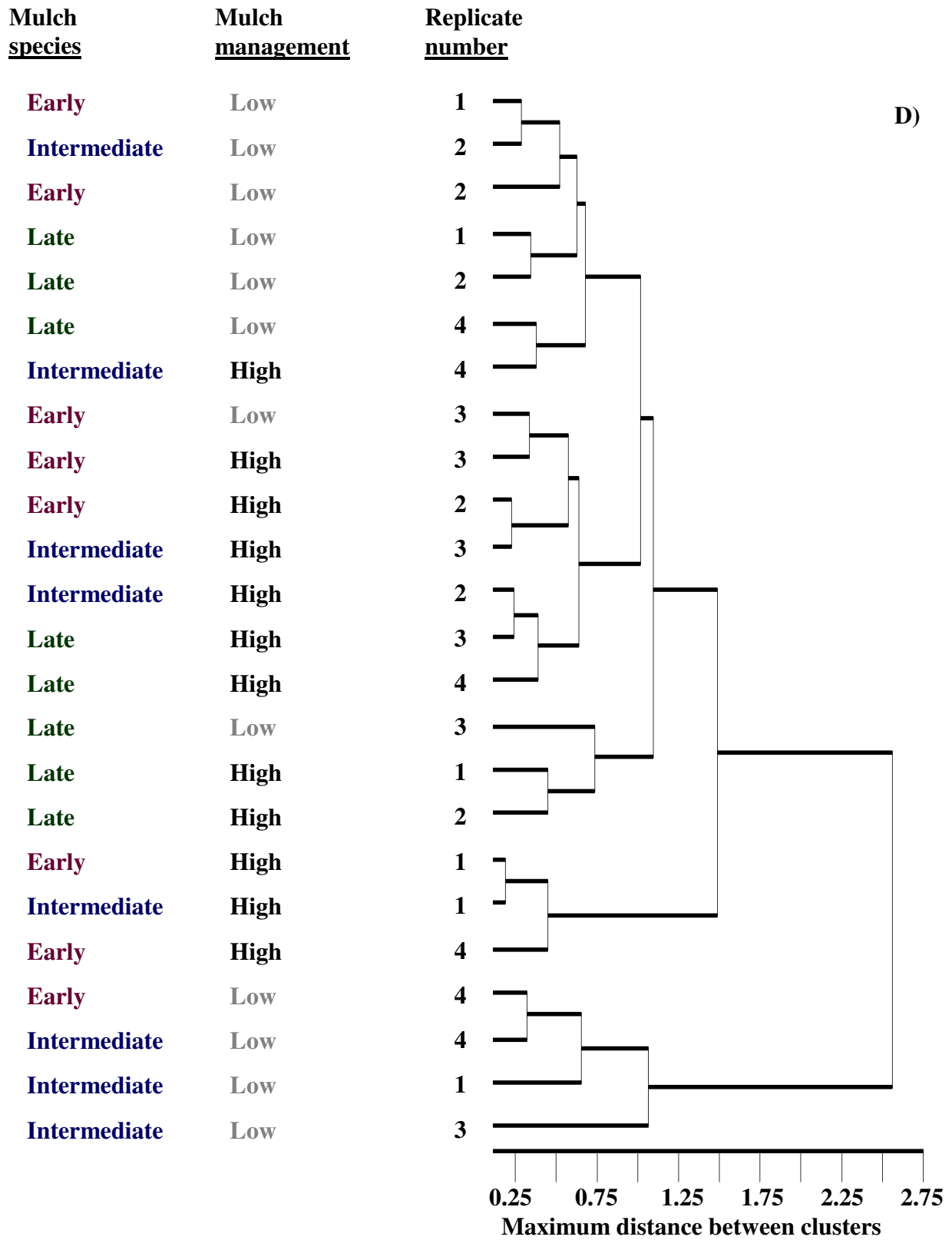
Supplementary Figure S1 (cont'd)



Supplementary Figure S1 (cont'd)



Supplementary Figure S1 (cont'd)



APPENDIX 1.2

RECORD OF DEPOSITION OF VOUCHER SPECIMENS

The specimens listed below have been deposited in the named museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number have been attached or included in fluid preserved specimens.

Voucher Number: 2013-04

Author and Title of thesis:

Author: Alexandria Bryant

Title: Influence of living and non-living habitat complexity on arthropods in strip-tilled cabbage

Museum(s) where deposited:

Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Specimens:

**If lowest taxonomic level is above family, lowest classification used for arthropod is indicated

Supplementary Table S5. Voucher specimens deposited at the Albert J. Cook Arthropod Research Collection (Michigan State University).

Family	Genus-Species	Life Stage	Quantity	Preservation
Anthocoridae	<i>Orius sp.</i>	Adult	1	Pinned
Aphididae	<i>Brevicoryne brassicae</i>	Mixture	multiple	Alcohol
Braconidae	<i>Cotesia rubecula</i>	Adult	12	Pinned
Cantharidae		Adult	1	Pinned
Carabidae	<i>Agonum cupripenne</i>	Adult	1	Pinned
Carabidae	<i>Amara sp.</i>	Adult	1	Pinned
Carabidae	<i>Anisodactylus sanctaecrucis</i>	Adult	1	Pinned
Carabidae	<i>Bembidion quadrimaculatum</i>	Adult	1	Pinned
Carabidae	<i>Bradycellus rupestris</i>	Adult	1	Pinned
Carabidae	<i>Cicindela sp.</i>	Adult	1	Pinned
Carabidae	<i>Colliurus pensylvanica</i>	Adult	1	Pinned
Carabidae	<i>Cyclotrachelus sodalist</i>	Adult	1	Pinned
Carabidae	<i>Harpalus erraticus</i>	Adult	1	Pinned
Carabidae	<i>Poecilus chalcites</i>	Adult	1	Pinned
Carabidae	<i>Pterostichus permundus</i>	Adult	1	Pinned
Carabidae	<i>Scarites quadriceps</i>	Adult	1	Pinned
Carabidae	<i>Stenolophus comma</i>	Adult	1	Pinned
Chrysomelidae	<i>Phyllotreta cruciferae</i>	Adult	1	Pinned
Chrysomelidae	<i>Phyllotreta striolata</i>	Adult	1	Pinned
Chrysopidae		Adult	1	Pinned
Chrysopidae		Larva	1	Alcohol

Supplementary Table S5 (cont'd)

Family	Genus-Species	Life Stage	Quantity	Preservation
Class Chilopoda		Adult	1	Alcohol
Coccinellidae	<i>Coccinella septempunctata</i>	Adult	1	Pinned
Coccinellidae	<i>Coleomegilla maculata</i>	Adult	1	Pinned
Coccinellidae	<i>Harmonia axyridis</i>	Adult	1	Pinned
Coccinellidae	<i>Hippodamia convergens</i>	Adult	4	Pinned
Coccinellidae	<i>Hippodamia parenthesis</i>	Adult	1	Pinned
Coccinellidae	<i>Propylea quatuodecimpunctata</i>	Adult	1	Pinned
Coenagrionidae		Adult	1	Pinned
Geocoridae		Adult	1	Pinned
Ichneumonidae	<i>Diadegma insulare</i>	Adult	1	Pinned
Lampyridae		Adult	1	Pinned
Libellulidae		Adult	1	Pinned
Mantidae		Nymph	1	Alcohol
Miridae	<i>Lygus lineolaris</i>	Adult	1	Pinned
Nabidae		Adult	2	Pinned
Noctuidae	<i>Melanchra picta</i>	Larva	2	Alcohol
Noctuidae	<i>Trichoplusia ni</i>	Larva	4	Alcohol
Pentatomidae	<i>Podisus maculiventris</i>	Adult	1	Pinned
Pentatomidae	<i>Podisus maculiventris</i>	Nymph	1	Alcohol
Phalangidae		Adult	1	Alcohol
Pieridae	<i>Pieris rapae</i>	Adult	2	Pinned
Pieridae	<i>Pieris rapae</i>	Larva	4	Alcohol
Plutella	<i>Plutella xylostella</i>	Adult	2	Pinned
Plutella	<i>Plutella xylostella</i>	Larva	4	Alcohol
Reduviidae		Adult	1	Pinned
Salticidae		Adult	1	Alcohol
Sphecidae		Adult	1	Pinned
Staphylinidae		Adult	1	Pinned
Superfamily				
Chalcidoidea		Adult	6	Pinned
Syrphidae		Larva	1	Alcohol
Tachinidae		Adult	1	Pinned
Tetragnathidae		Adult	1	Alcohol
Thomisidae		Adult	1	Alcohol
Vespidae		Adult	1	Pinned

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