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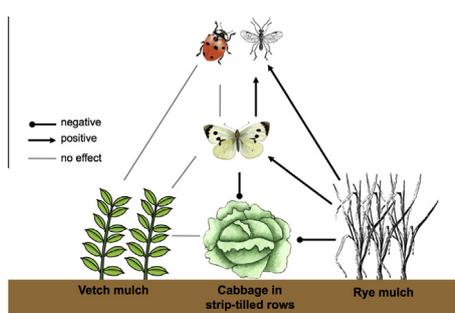
Perspective

Cover crop mulches influence biological control of the imported cabbageworm (*Pieris rapae* L., Lepidoptera: Pieridae) in cabbageAlexandria Bryant^a, Thomas Coudron^b, Daniel Brainard^c, Zsofia Szendrei^{a,*}^a Department of Entomology, 288 Farm Lane, Room 243, Michigan State University, East Lansing, MI 48824, USA^b USDA-Agricultural Research Service, Biological Control of Insects Research Laboratory, 1503 South Providence Road, Research Park, Columbia, MO 65203, USA^c Department of Horticulture, A288 Plant and Soil Science Bldg., Michigan State University, East Lansing, MI 48824, USA

HIGHLIGHTS

- We studied the impact of cover crop mulch on imported cabbageworm biocontrol.
- Cover crop mulch species affected cabbageworm and *Cotesia rubecula* abundance.
- Increased parasitoid abundance did not result in increased parasitism in the field.
- Mulch interfered with the short-range host finding odor cues of *Cotesia rubecula*.
- Small natural enemies provide biological control of the imported cabbageworm.

GRAPHICAL ABSTRACT



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ABSTRACT

Increasing structural complexity within crop fields can provide a way to manipulate pest abundance and biological control in agroecosystems. Here, we examine the effect of cover crop mulches in cabbage on the structure and function of an insect food web, investigating the role of cover crop species, structure, and volatile cues on important interactions. We focused on the imported cabbageworm (*Pieris rapae* L., Lepidoptera: Pieridae), and three of its natural enemies, the spined soldier bug (*Podisus maculiventris* (Say), Hemiptera: Pentatomidae), the convergent lady beetle (*Hippodamia convergens* (Guerin), Coleoptera: Coccinellidae), and the parasitoid, *Cotesia rubecula* Marshall (Hymenoptera: Braconidae). We measured the abundance of these insects in a field experiment and conducted a natural enemy exclusion cage study to determine the level of biological control of the imported cabbageworm in the field. Our field experiments indicated that cover crop species, but not structure, influenced insect abundance, with significantly more imported cabbageworm and *C. rubecula* in rye cover crop mulch plots compared to vetch mulch or bare soil plots. In the Y-tube assays we found some evidence that the increased parasitoid abundance did not result in increased parasitism because of interference of the mulch with short-range host finding odor cues. The natural abundance of the two predators was not different among our field plots with different cover crop treatments. Mortality and parasitism of sentinel imported cabbageworm larvae was not different in field cages among the different cover crop mulch treatments, but there was a significant difference among cage types indicating that small natural enemies play an important role in the biological control of this cabbage pest.

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1. Introduction

Habitat management techniques such as cover cropping can manipulate in-field structural complexity to affect pests and their natural enemies (Altieri and Letourneau, 1982; Schmidt et al., 2004, 2007; Lundgren and Fergen, 2010, 2011). The addition of cover crops to vegetable rotations can potentially have positive, neutral or even negative effects on both pests and their natural enemies, suggesting that cover crops can affect whole food webs in multiple ways. These effects can in turn be mediated through changes in structural complexity or changes in volatile cues used by pests and natural enemies to locate food plants and prey. Here, we examine the effect of cover crop mulches on the structure and function of an insect food web in cabbage, investigating the role of cover crop species, structure, and volatile cues on trophic interactions.

Killed cover crop mulches, as a way to increase in-field structural complexity, are of interest to vegetable producers because they can be easily incorporated into annual, rotated cropping systems, can eliminate plant–plant competition with the main crop and, have numerous horticultural benefits (Haramoto and Brainard, 2012). In general, structurally complex habitats may provide alternative prey, enhance efficiency of predators, and provide protection from intraguild predators (Langellotto and Denno, 2004). The plant residues that killed cover crops leave behind can reduce insect pest abundance in cabbage fields (Mangan et al., 1995; Bottenberg et al., 1997; Xu et al., 2011). 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 that mulching can impact conservation biological control within the field.

Within-field structural complexity can be manipulated through the management of cover crop mulches. In cover cropped, strip-tilled systems, mulches remain between crop rows and can be rolled or crimped to reduce vertical complexity, while creating dense mulch habitat along the soil surface. Rolled mulch can reduce soil temperatures but has a mixed effect on cabbage yields, while its impact on natural enemies is unknown (Mochizuki et al., 2008). In one case, Laub and Luna (1992) found that standing cover crop mulch in corn led to greater natural enemy abundance (e.g. ground dwelling predators) compared to plots with cover crop mulch lying on the soil surface. However, mulching management strategies that manipulate habitat height between cabbage rows have never been examined for their impacts on biological control.

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; Randlkofer et al., 2010). Chemical cues appear to play a particularly important role in the attraction of natural enemies to locate herbivores within a cabbage field (Agelopoulos and Keller, 1994b). Feeding damage and frass from the imported cabbageworm (*Pieris rapae* L., Lepidoptera: Pieridae) larvae release a blend of volatiles into the surrounding environment (Agelopoulos and Keller, 1994a,c; Mumm et al., 2008). These resource-indicating odors specify the presence and location of the imported cabbageworm to natural enemies (Schroeder and Hilker, 2008) and determine differences in behavior between generalist and specialist natural enemies (van Poecke et al., 2003; Vuorinen et al., 2004). Complex habitats create a greater diversity of background odors in the environment. Schroeder and Hilker (2008) have found that background odors can be: (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. Yet, it is unknown how background odors from decaying cover crop mulches influence natural enemies.

The primary goals of this study were to examine the impacts of cover crop species (a legume and a cereal) and management (crimping or no-crimping) on insects in cabbage. Secondary objectives included assessment of weed abundance and diversity as well as crop yield. We focused on a pest, the imported cabbage cabbageworm (*P. rapae*, Lepidoptera: Pieridae), and three of its natural enemies that are commonly present in temperate-zone cabbage fields. We measured the abundance of insects in a field experiment and conducted a natural enemy exclusion cage study to determine the level of biological control of the imported cabbageworm in the field. We also conducted a Y-tube assay to determine the role of volatiles as a possible mechanism for the observed results from the field.

2. Materials and methods

2.1. Experimental design and field operations

A field study was established at Michigan State University's Horticulture Farm in East Lansing, Michigan (42.673872, -84.485044). The experiment was a randomized complete block design with six treatments and four replications. Treatments consisted of combinations of two factors: mulch species (bare soil, vetch, or rye) and management (none or crimping between cabbage rows). On October 4, 2011 cover crop seeds were broadcast by hand into 9.14 × 9.14 m plots. Winter rye (*Secale cereale*; Dirt Works, New Haven, VT) was broadcast at a rate of 183 kg/ha and hairy vetch (*Vicia villosa*; Johnny's Selected Seeds, Albion, ME) at a rate of 61 kg/ha. On April 27, 2012 Select Max (clethodim, 0.18 L/ha a.i.) 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[®] (glyphosate, 3.03 L/ha a.i.) was applied on May 11 followed by an application of Stinger[®] (clopyralid, 0.58 L/ha a.i.), applied on May 22 to effectively kill the vetch cover crop. Due to the dense biomass in vetch plots, we used a push mower (DR[®] Trimmer; Vergennes, VT), to allow the 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 wide and 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 (N–P–K) fertilizer was applied in planting rows at this time (Warncke et al., 2004). Strip tillage left 80 cm strips of cover crop residue undisturbed between planting rows. After tillage, plots assigned to crimping treatments were crimped by manually pulling a plywood rectangle (76 × 25 cm) equipped with rope handles over the cover crop residue between rows. This method effectively crimped the standing mulch in the case of both cover crop species.

Cabbage transplants (var. "Blue Dynasty"; Siegers Seed Company, Holland, MI) were grown for 4 weeks in 98 cell plug trays and transported to the Horticulture Farm to harden off 15 days prior to transplanting in the field. Cabbage was transplanted by hand beginning on May 29 into strip-tilled zones with 36 × 76 cm spacing. Each experimental plot consisted of 12 rows of cabbage, and two buffer rows were planted along the edges of the field.

Fungicides and insecticides were not used during the course of the growing season, but herbicides included GoalTender[®] 4SC (oxyfluorfen, 1.72 L/ha a.i.) and Select Max[®] (clethodim, 0.18 L/ha a.i.) was 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) and additional hand-weeding was performed in all plots to reduce weed pressure further.

2.2. Mulch, weed, and cabbage measurements and analyses

Cabbage was harvested beginning on September 5. In each plot, cabbage heads were harvested from the middle 4.6 m of the central 8 rows. The number and weight of marketable and non-marketable heads were assessed, based on the USDA size standard of 0.45 kg and higher as marketable. Cabbage heads greater than 11.4 cm (e.g.; ca. 0.45 kg) in diameter were considered marketable yield.

Mulch height and biomass were measured 3 times during the growing season, on June 18, August 8, and September 4. Mulch height was measured in two 0.25 m² quadrats randomly distributed in each plot. Within each quadrat, we made ten height measurements and collected mulch biomass. Prior to weighing, all above ground mulch biomass was dried in a drying oven at 60 °C for 7 days.

A weed census was also conducted 40 days prior to hand-weeding, on June 20, and 8 and 36 days after hand-weeding, on August 8 and September 11 respectively. Within the 0.25 m² quadrats, weeds were counted and identified to species. Based on census data, weed identity, 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 pennsylvanicum* L.), common ragweed (*Ambrosia artemisiifolia* L.), redroot pigweed (*Amaranthus retroflexus* L.), and wild radish (*Raphanus raphanistrum* L.). Weed height, weed diversity, and marketable cabbage yield were included as covariates in models examining insect abundance.

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, weed height, and weed species richness. For analysis, mulch height measurements were averaged across quadrats for each plot, while mulch biomass was summed across quadrats. Mulch height and biomass were transformed sqrt ($x + 0.5$) to meet assumptions of normality and equal variance. For all mulch and weed variables, an analysis of variance was performed with a model including mulch species, mulch management, and their interaction as fixed factors and block as a random factor. A least-square means test with Tukey–Kramer adjustment was performed if main effects or their interactions were significant ($\alpha = 0.05$).

2.3. Arthropod sampling and analyses

To determine the effect of mulch species and management on arthropod abundance, imported cabbageworm larvae and spined soldier bugs (*Podisus maculiventris* (Say), Hemiptera: Pentatomidae) were visually sampled on all the leaves of 10 randomly chosen cabbage plants per plot, starting on June 13 and ending on August 29, 2012. The 10 plants per plot were randomly chosen from central rows to eliminate edge effects. Convergent lady beetle (*Hippodamia convergens* (Guerin), Coleoptera: Coccinellidae), and *Cotesia rubecula* Marshall (Hymenoptera: Braconidae) were sampled with yellow sticky traps on metal stakes (7.5 × 12.3 cm, Great Lakes IPM, Vestaburg, MI) during the same time period as the visual sampling. One sticky trap was placed into the center of each plot, 0.4 m above the soil surface and changed weekly. We chose to focus on the four insect species because they are annually present and relatively abundant in cabbage fields in Michigan (Z. Szendrei unpublished results). In addition to recording the number of the four focal species in our experimental field, we also recorded the abundance of other arthropods using the two types of surveys described above. Herbivore, predator and parasitoid abundance were measured on sticky traps or 10 plants per plot weekly throughout the growing season (Supplementary data Table S5–S8). From this data

we created three variables: average predator, parasitoid and, herbivore abundance per plot for each sampling date and used these as covariates in the statistical analyses to account for biotic factors in the field.

Abundance data from insect sampling was transformed using $\log(x + 0.01)$ to meet normality assumptions and analyzed with a repeated measures analysis. Statistical 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. If main effects were significant ($\alpha = 0.05$), we performed least-square means tests with Tukey–Kramer adjustment.

2.4. Natural enemy exclusion cages

To determine treatment effects on biological control services provided by different natural enemy groups (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 and each cage consisted of an 8 wk old cabbage plant in a 15.2 × 14 cm (diameter × height) pot with Sure-Mix Perlite (Michigan Grower Products, Galesburg, MI). Two 0.9 m wires were bent in a U-shape and the two ends were submerged into the potting soil to create a wire framework, which supported the mesh. The pots of the caged plants were submerged in the soil in the field plots and four first instar imported cabbageworm were transferred to the caged plants. Imported cabbageworms were taken from a greenhouse colony kept at Michigan State University. The colony originated from the Horticulture Farm (East Lansing, MI) and had been maintained for ca. 10 generations in the greenhouse. Insects were kept in 47.5 × 47.5 × 93 cm mesh bug dorm cages (Megaview Science Co., Ltd., Taichung, Taiwan) with a 16:8 h 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).

The first type of 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 at the top of the pot. Any mortality of prey in this cage could be associated with natural mortality due to environmental conditions or handling. The second type of cage had white mosquito netting (Skeeta Company, Bradenton, FL) with 2 mm openings, allowing parasitoids and small predators access to the sentinel prey but excluding larger predators, such as predatory stink bugs and lady beetles. The third cage type, a sham cage, was identical to the mosquito-netting cage, however, it was not closed with a rubber band at the top of the pot, but the netting was raised 1 cm above the soil surface allowing ground predators access to the sentinel prey. This type of netting also allowed larger predators access through 10 rectangular openings (3 × 20 cm) cut into 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 36 h, after which predators were removed and plants were re-covered with a fine mesh. Any remaining imported cabbageworm larvae were reared on cabbage plants until parasitoid or butterfly pupae or adults were observed. Predation and parasitism rates were calculated based on larvae killed or parasitized. The exclusion cage experiment was repeated 3 times during the growing season starting on June 28, July 30, and August 23.

Mortality and parasitism percentages were transformed using arcsin ($x + 0.5$) 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 ($\alpha = 0.05$).

2.5. Y-tube olfactometer assays

For the Y-tube assays, imported cabbageworm larvae were taken from the greenhouse colony described above. Third instar spined soldier bugs were from a colony reared at the 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 Y-tube assays upon arrival.

Adult convergent lady beetles were purchased from Rincon-Vitova Insectaries (Ventura, CA). Beetles were placed in petri dishes (150 × 15 mm; VWR, Radnor, PA) and fed a 10% honey solution upon arrival. Subsequently, beetles were held at 10 °C until needed for assays, they were removed from the fridge 24 h prior to the start of an assay and kept in the laboratory at 25 °C.

C. rubecula were reared in a greenhouse colony at Michigan State University. Parasitoids were originally collected from the Horticulture Farm (East Lansing, MI) in summer 2012 and maintained in the greenhouse for 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 feeding on cabbage plants for 24 h prior to use in Y-tube assays. To eliminate any effects that the sex of the parasitoid may have on odor preference, only female *C. rubecula* were used in Y-tube assays.

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; see Table 1 for list of treatments). Each odor source consisted of an outer pot (14 cm diameter × 12 cm height) with a smaller inner pot (8 × 9 cm) placed inside. 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 cabbage, the inner pot contained three cabbage plants. Cabbage seedlings (*B. oleracea* var. “Farao”; Johnny's Selected Seeds, Albion, ME) were grown for 1 month in the greenhouse (16:8 h L:D; 23–28 °C) before transplanting three cabbage plants into a 8 × 9 cm pot together. Cabbage plants were grown

Table 1
List of treatments for the Y-tube choice tests performed for three natural enemies of the imported cabbageworm (spined soldier bug, convergent lady beetle, and *Cotesia rubecula*). Damaged cabbage refers to three cabbage plants in a pot that were fed on by six 5th instar imported cabbageworms for 24 h.

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

in separate pots from mulch species to prevent any confounding effects or interactions between mulch and cabbage plants.

For odor sources with mulches, rye, hairy vetch, or both species were planted in the space between the inner and outer pots. Rye was planted at a rate of 7 g/pot. Hairy vetch was planted at a rate of 4 g/pot. The same rye and vetch varieties were used as in the field experiments. Mulch species were planted at these same rates for odor sources containing both rye and vetch. After 1 month, RoundUp® (glyphosate, 3.03 L/ha a.i.) 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 × 30 × 30 cm; Bioquip Products, Rancho Dominguez, CA). At this time, all inner pots were placed within outer pots. To create herbivore damage on cabbage, six 5th instar imported cabbageworm were placed on the three cabbage plants in the inner pots and allowed to feed for 24 h.

To test olfactory preferences of the spined soldier bug, convergent lady beetle, and *C. rubecula*, a Y-tube olfactometer was used (two 6 cm arms and one 12 cm arm, 2 cm diameter, ground glass joints; Michigan State University Glass Blowing Facility, East Lansing, MI). Air filtered through activated charcoal was divided into two streams, each traveling in Teflon® tubing leading to two glass chambers (7 L each; Corning Incorporated, Corning, NY). One arm contained clean air, while the other contained one of the treatment odors (Table 1). Airflow was adjusted for each natural enemy species and maintained at 1 L/min for both adult convergent lady beetles and *C. rubecula* adults. However, airflow was reduced for spined soldier bugs to 0.5 L/min (Vuorinen et al., 2004).

Individual natural enemies were placed at the bottom of the Y-tube and observed for 15 min or until a choice was made. Once the insect moved past the mid-point of one of the shorter arms of the Y-tube, the insect was removed and the choice recorded. If an insect did not respond within 15 min, 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 then hexane before drying at 60 °C. Each treatment was replicated 28–48 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.

3. Results

3.1. Cabbage yield

Cabbage yields were significantly lower in rye plots but were unaffected by mulch management (crimping) treatments (Supplementary data Table S1). Marketable ($t = 0.16$, $df = 15$, $P = 0.99$) and non-marketable yields ($t = 0.28$, $df = 15$, $P = 0.96$) did not differ among bare soil and hairy vetch plots. However, 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, yields were lowest in rye plots with 1.5 times more unmarketable cabbage biomass compared to bare soil or vetch plots ($t > 3.11$, $df = 15$, $P < 0.02$).

3.2. Mulch and weed measurements

Our treatments created habitats with diverse structural complexity as indicated by the significantly taller mulch height in

non-crimped rye plots compared to the height in vetch ($t > 7.40$, $df = 15$, $P < 0.02$) or bare soil plots ($t > 9.30$, $df = 15$, $P < 0.01$), (Supplementary data Table S2). Mulch height in vetch plots was not significantly different from bare soil plots throughout the growing season ($t = 1.88$, $df = 15$, $P > 0.08$). 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 3, 11, and 4 times taller in non-crimped compared to crimped plots during the early, intermediate, and late portions of the season respectively (Supplementary data Table S2).

Mulch biomass differed across mulch species with the greatest amount of biomass in rye plots throughout the growing season (Supplementary data Table S3). Vetch residue had almost completely decomposed by the intermediate sampling date, while rye residue persisted 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 ($t > 4.56$, $df = 18$, $P < 0.01$).

Average weed height during the season was significantly reduced in plots with rye mulch, 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 density and species richness were 2 times and 50% greater in bare soil plots respectively compared to rye mulch plots ($t > 3.19$, $df = 15$, $P < 0.02$; Supplementary data Table S4).

3.3. Arthropod abundance

The focal insect species' abundances were similar between crimped and non-crimped plots, but cover crop species significantly influenced the abundance of imported cabbageworm and *C. rubecula*. Mulch management (crimping) did not influence the abundance of the imported cabbageworm ($F = 0.49$, $df = 1,18$; $P = 0.49$), spined soldier bug ($F = 0.54$, $df = 1,23$; $P = 0.47$), convergent lady beetle ($F = 0.00$, $df = 1,19$; $P = 0.97$), or *C. rubecula* ($F = 0.27$, $df = 1,20$; $P = 0.61$). Cover crop mulch species significantly influenced the abundance of imported cabbageworm ($F = 5.72$, $df = 2,22$; $P = 0.01$; Fig. 1A) and *C. rubecula* ($F = 18.58$, $df = 2,23$; $P < 0.01$; Fig. 1B), but this was not consistent over time (date by cover crop interaction: ($F > 7.96$, $df = 30, 243$; $P < 0.01$). Over the growing season, imported cabbageworms 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 ($t = 4.91$, $df = 23$, $P < 0.01$). The specialist parasitoid, *C. rubecula*, was approximately two times more abundant in rye mulched plots compared to plots with bare soil ($t = 5.85$, $df = 26$, $P < 0.01$) and 34% more abundant in rye compared to vetch treated plots ($t = 4.72$, $df = 24$, $P < 0.01$). Contrary to our specialist parasitoid, the abundance of the two generalist predators, the spined soldier bug ($F = 2.08$, $df = 2,25$; $P = 0.15$) and the convergent lady beetle ($F = 0.02$, $df = 2,19$; $P = 0.98$), were not impacted by mulch species.

Several covariates were significant in our model, potentially influencing abundance of arthropods. Greater weed height was negatively associated with abundance of imported cabbageworm ($F = 23.34$; $df = 1,213$; $P < 0.01$). Weed diversity was positively associated with the abundance of spined soldier bug ($F = 9.07$, $df = 1,166$; $P < 0.01$), but convergent lady beetle abundance was not associated with any of the covariates we examined. Weed height was negatively associated with the abundance of *C. rubecula* ($F = 42.84$, $df = 1,219$; $P < 0.01$) and *C. rubecula* abundance was positively impacted by the abundance of its host ($F = 76.39$, $df = 1,230$; $P < 0.01$). The increase in imported cabbageworm abundance was proportional to the increase in *C. rubecula* abundance in rye plots relative to the two other treatments, vetch and bare soil, with about 1.3-fold increase for both species (Fig. 1A and B).

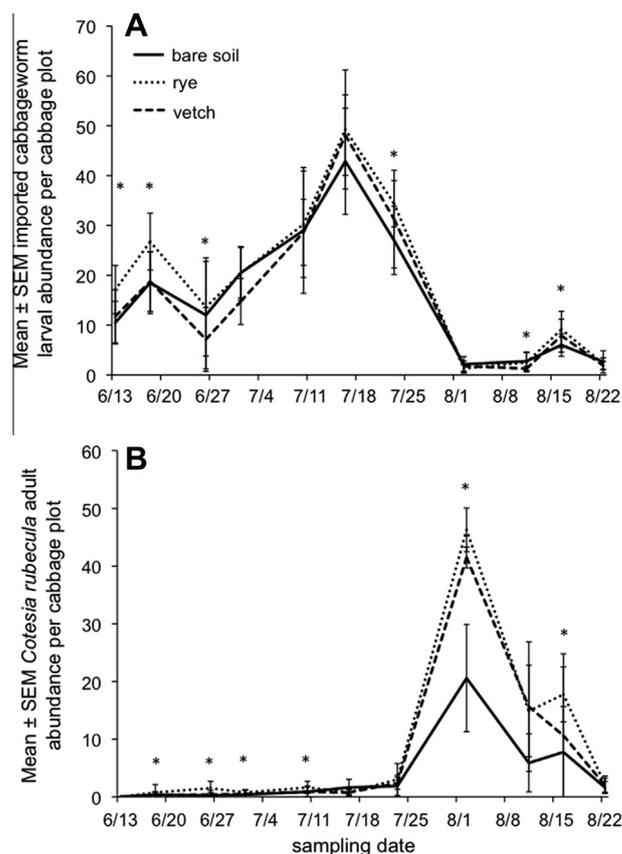


Fig. 1. Insect abundance (mean \pm SEM) in experimental cabbage field plots planted into bare soil, hairy vetch mulch, or rye mulch. Imported cabbageworm larvae (A) were visually sampled on 10 randomly chosen cabbage plants per plot for 11 weeks during the growing season. *Cotesia rubecula* (B) were sampled with yellow sticky traps for 10 weeks during the growing season in 2012. Asterisks denote significant differences within a given date among the three cover crop mulch treatments ($\alpha = 0.05$).

3.4. Natural enemy exclusion cages

Mortality rates of the sentinel prey in the cages were significantly different across cage types at each sampling date ($F > 18.51$; $df = 3,54$; $P < 0.01$; Fig. 2A). The no-see-um netting cages effectively excluded all natural enemies with mortality rates between 1% and 5% during the season. Predators and parasitoids were not observed inside these cages, suggesting that loss of larvae was due to natural mortality. 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% to 89% in cages that allowed natural enemy access. Dead caterpillars were rarely recovered and it is possible that in addition to consumption by natural enemies larvae also moved off the plants. 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 ($t < 1.59$, $df = 54$, $P > 0.12$; Fig. 2A) that allowed all natural enemies access to the prey, suggesting the majority of larval predation is due to the small predator guild.

The no-see-um netting cage effectively excluded parasitoids, with no parasitism observed (Fig. 2B). 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 ($F > 8.59$; $df = 3,54$; $P < 0.01$; Fig. 2B). During the intermediate and late season sampling dates, parasitism rates in the mosquito,

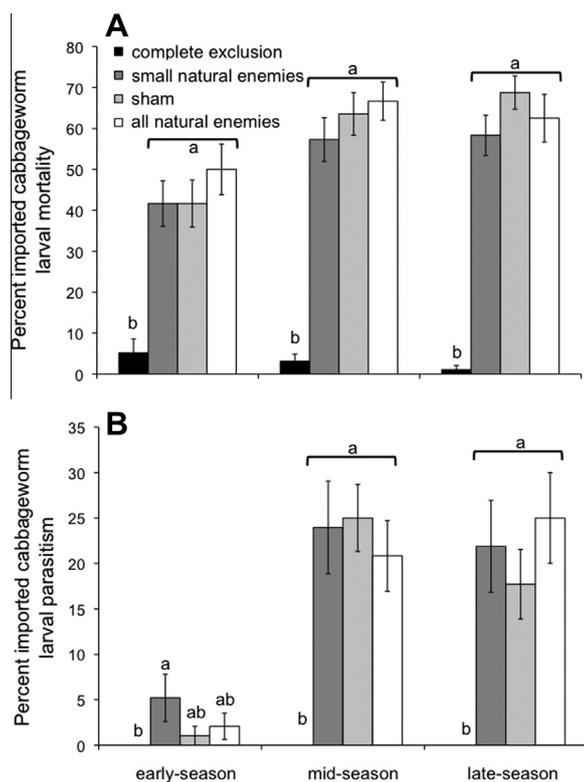


Fig. 2. Percent (mean \pm SEM) mortality (A) and parasitism (B) of the imported cabbageworm across different types of natural enemy exclusion cages placed into an experimental cabbage field. Bars with different letters are significantly different from each other ($\alpha = 0.05$).

sham, and no-netting cages, which allowed parasitoids access to the larvae, were significantly greater than the no-see-um cages, which excluded the parasitoids ($t > 3.24$, $df = 54$, $P < 0.01$). Parasitism rates ranged from 18% to 25% later in the growing season.

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 ($F < 0.63$; $df = 3,54$; $P > 0.60$), indicating that larval mortality due to different natural enemy guilds was unaffected by mulch species or management treatments. This trend was also true for imported cabbageworm parasitism, where the interaction between cage type and mulch species ($F < 2.13$; $df = 6,54$; $P > 0.06$) or cage type and mulch management treatments ($F < 1.34$; $df = 3,54$; $P > 0.27$) was also not significant.

3.5. 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* moved down one arm of the olfactometer, allowing a choice to be recorded (Fig. 3). None of the three tested natural enemies were attracted to rye mulch, vetch mulch, or both hairy vetch and rye mulch compared to clean air ($G_{adj} < 3.47$, $df = 1$, $P > 0.05$).

When given a choice between clean air and damaged cabbage, the spined soldier bug ($G_{adj} = 0.91$, $df = 1$, $P = 0.34$; Fig. 3A) and the convergent lady beetle ($G_{adj} = 0.58$, $df = 1$, $P = 0.45$; Fig. 3B) did not prefer either odor source. Additionally, the generalist predators were not attracted to damaged cabbage compared to rye mulch, vetch mulch, or both rye and vetch mulch ($G_{adj} < 1.38$, $df = 1$, $P > 0.24$; Fig. 3A and B). 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 by 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 ($G_{adj} = 12.31$, $df = 1$, $P < 0.01$; Fig. 3C). 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 ($G_{adj} = 10.45$, $df = 1$, $P < 0.01$).

4. Discussion

Contrary to expectations, we found evidence that addition of a rye mulch led to increased imported cabbageworm abundance in field plots, which was coupled with an increase in abundance, but not effectiveness, of its specialist parasitoid, *C. rubecula*. In a previous study, imported cabbageworm abundance was lower in cabbage with rye mulch compared to non-mulched plots (Bottenberg et al., 1997). Banks (1998) suggested that imported cabbageworm is unresponsive to within field complexity due to its high mobility and widespread oviposition patterns and, that any difference in its abundance across habitats of varying complexity is likely due to biological control. Root and Karieva (1984) found a similar result where collards interplanted with potatoes had similar numbers of imported cabbageworm eggs as collards in monoculture. On the other hand, studies conducted by Latheef and colleagues (Latheef and Irwin, 1979; Latheef and Ortiz, 1983) indicated that the imported cabbageworm increased its oviposition and damage in collard plots interplanted with different species of herbaceous plants. In our field plots we observed a similar outcome, with generally higher imported cabbageworm abundance in cover crop mulched than bare soil cabbage plots, although this trend varied through the season. Thus we did not find support for Root's (1973) resource concentration hypothesis, which predicted that herbivores, especially herbivores with narrow host range, would be more abundant in pure stands. The abundance of the imported cabbageworm and *C. rubecula* were positively correlated, and, although parasitoids were more abundant in rye-mulched plots, they were not able to suppress populations of the pest. Parasitoids preferentially land on and search plants with imported cabbageworm feeding damage (Agelopoulos and Keller, 1994b), therefore mulching with rye may be indirectly supporting higher *C. rubecula* populations through increased host abundance. In our Y-tube assays we found some evidence that this increased parasitoid abundance did not result in increased parasitism because of interference of the mulch with short-range host finding odor cues. Additional factors that may lead to increased abundance of *C. rubecula* in rye-mulched plots could be the provisioning of attractive microclimates and protection from its natural enemies.

Mulch management and species did not influence the abundance of the two generalist predators we focused on, the spined soldier bug and the convergent lady beetle. It is likely that canopy-foraging predators, such as the ones we focused on, are less likely to show a response to mulching than ground predators (e.g. Riechert and Bishop, 1990). The presence of cover crop mulch may interfere with the mobility of predators searching for prey, reducing their efficiency (Legrand and Barbosa, 2003; Tylianakis and Romo, 2010). Complex habitats have been shown to interfere with visual (Ferran and Dixon, 1993) or chemical (Randlkofer

responses of generalist and specialist herbivores are known to exist due to the variability of glucosinolate concentrations in brassica cultivars (Giamoustaris and Mithen, 1995; Li et al., 2000). In our study, convergent lady beetles and spined soldier bugs were not attracted to damaged cabbage, although these two species have been shown to prefer herbivore damaged plants in previous studies (Hamilton et al., 1999; Sant'Ana et al., 1999; Acar et al., 2001). This difference between current and previous findings may be due to the inability of these species to discriminate resource-indicating odors with the cabbage cultivar used here (Vuorinen et al., 2004) or their need for a bouquet of resource-indicating odors from multiple species of 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) or they may need to learn to associate host odor cues before responding to them (e.g. De Boer and Dicke, 2000; Drukker et al., 2000; Glinwood et al., 2011).

The background odors of rye and vetch mulch were neither attractive nor repellent to the two predator species tested here. This could be because they may not be able 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.

In summary, this research found that cover crop mulch species choice in cabbage fields may be an important factor to consider when using it as a conservation biocontrol tool, and that the community of small predators in the field is important for imported cabbageworm biocontrol. In addition, our results suggest that traits of cover crop mulches, such as odor cues, can have a significant role in determining the outcome of interactions between pests and natural enemies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2014.03.012>.

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