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Habitat manipulation of the apple orchard floor to increase ground-dwelling predators and predation of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae)

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Abstract

Augmenting generalist predator populations in new apple (*Malus domestica* Bork) plantings could potentially aid in the establishment of balanced orchard ecosystems that are less susceptible to pest outbreaks. Habitat can be an important factor in retaining predators in a system and can affect predator efficiency. We investigated the potential of increasing a complex of generalist ground-dwelling predators and enhancing biological control in a young 'Golden Delicious' apple orchard through ground habitat manipulation. We modified the orchard floor with four comparative habitat treatments: (1) detritus-rich compost mulch layer, (2) detritus-free synthetic mulch layer, (3) herbicide-treated vegetation thatch, and (4) bare soil with vegetation hand-removed. Relative abundances of predators and alternative prey in the habitats were measured with pitfall trapping throughout the growing season. Predation was measured using sentinel *Cydia pomonella* larvae and directly observed in night experiments. Throughout the season, the compost mulch treatment consistently supported significantly greater densities of alternative prey resources for predators, and generalist predators were more abundant in the compost mulch than the other habitats. Predator complex abundance was positively correlated with increasing alternative prey availability in the compost mulch habitat. However, predation of *C. pomonella* was significantly lower in the compost mulch than in the herbicide-treated thatch habitat. Our study revealed that a prey-rich organic mulch can enhance ground-foraging generalist predators on the orchard floor, but habitat structure may be more important than alternative prey for predation of *C. pomonella*.

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Keywords: Ants; Apple; *Malus domestica*; *Cydia pomonella*; Carabidae; Compost; Formicidae; Ground beetles; Habitat; Prey resources; Biological control

1. Introduction

Some pests of apple (*Malus domestica* Bork) in eastern North America, including codling moth (*Cydia pomonella* L.), apple maggot (*Rhagoletis pomonella* Walsh), plum curculio (*Conotrachelus nenuphar* Herbst), tufted apple bud moth (*Platynota idaeusalis* Walker), and woolly apple aphid (*Eriosoma lanigerum* Hausmann), spend a portion of their life cycle on the orchard floor where they are exposed to ground-

dwelling predators (Hogmire, 1995; Jaynes and Marucci, 1947; Schoene and Underhill, 1935). Generalist predators such as spiders (Arachnida: Araneae), ground beetles (Coleoptera: Carabidae), ants (Hymenoptera: Formicidae), and staphylinids (Coleoptera: Staphylinidae) that reside on the orchard floor feed on a range of prey, including aphids and the pupae and larvae of lepidopterous and dipterous apple pests (Allen, 1979; Allen and Hagley, 1990; Hagen, 1987; Hagley and Allen, 1988; Lovei and Sunderland, 1996; Riddick and Mills, 1994; Riechert and Harp, 1987; Stradling, 1987; Way and Khoo, 1992).

Increasing evidence suggests that complexes or assemblages of ground-foraging generalist predators may

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exhibit synergistic pressures against prey populations (Chang, 1996; Ehler, 1990; Losey and Denno, 1998; Provencher and Riechert, 1994; Riechert and Bishop, 1990; Riechert and Lawrence, 1997). Enhancing an assemblage of generalist predators, rather than a single species, in apple orchards has potential for increasing biological control of the diverse and multi-generation apple pest complex (Brown and Adler, 1989). The establishment and retention of a generalist predator assemblage could be particularly important in developing a balanced agroecosystem and preventing pest outbreaks in newly planted orchards not yet colonized by pests.

A potential means of enhancing the ground-dwelling generalist predators is by manipulating the ground habitat that they use for mating, resting, shelter, and sources of alternative prey. Orchard floor management practices may affect both the habitat's physical structure and the alternative prey (Huffaker, 1958; Murdoch, 1969; Price, 1976; Root, 1973). Practices that disturb ground habitat structure, such as tilling and disking, generally disrupt predators in a range of cropping systems including apple (House and Brust, 1989; Laub and Luna, 1992; Stinner and House, 1990; Wilson-Rummenie et al., 1999). Conversely, increasing ground habitat complexity or structure has enhanced ground predators (Carcamo and Spence, 1994; Döbel and Denno, 1994; Lys, 1994; Uetz, 1991). The importance of habitat to generalist predators may also be related to their microclimate needs or their need for shelter from predators (Honek, 1997a,b; Riechert and Harp, 1987; Stradling, 1987; Thiele, 1979).

The addition of organic amendments such as composts, plant-derived mulches, or animal manures to the ground has increased generalist predators in several agricultural systems (Badejo et al., 1995; Brust, 1993; Culliney and Pimentel, 1985; Larsen et al., 1996; Litsinger and Ruhendi, 1984; Morris, 1922; Pimentel and Warneke, 1989; Riechert and Bishop, 1990). In addition, increased predation following mulch application has been shown for spiders in a mixed vegetable crop (Riechert and Bishop, 1990) and for ground beetles in potatoes (Brust, 1993).

Increases in predator densities following the addition of organic amendments to the ground may be related to the profusion of detritivores and fungivores, including mites and Collembola, that are associated with organic amendments (Badejo et al., 1995; Gill, 1969; Huhta et al., 1979; Morris, 1922; Pimentel and Warneke, 1989). These organisms are potential prey items for generalist predators such as ants, spiders, and ground beetles that feed on small arthropods (Bauer, 1982; Hengeveld, 1980; Lovei and Sunderland, 1996; Riechert and Harp, 1987; Snyder and Wise, 2001; Stradling, 1987; Way and Khoo, 1992; Wise, 1993). The link between "bottom-up" prey resources in the habitat and predator abun-

dance has been demonstrated in a few systems (Chen and Wise, 1999; Settle et al., 1996), but the importance of such detritivore–predator links to the biological control of herbivores has not been established.

This study investigated the potential of adding organic mulch to apple orchards to increase ground-dwelling generalist predators and subsequent predation of codling moth, a key pest of apple. We used comparative ground treatments that varied with respect to prey availability and physical structure to explore the relative importance of resources versus habitat structure to the predator complex. To compare predation in the ground treatments, we introduced fifth instar codling moth that typically wander on the orchard floor in search of pupation sites. Mathews et al. (2002) reported results specific to horticultural aspects of this study, with emphasis on tree vigor, substrate microclimate, weed growth, and arboreal and edaphic arthropod incidence.

2. Materials and methods

The research was conducted at the US Department of Agriculture, Appalachian Fruit Research Station, Kearneysville, WV during 1997 and 1998.

2.1. Identifying the generalist predator complex in apple

Pitfall sampling was conducted in 1997 in two 0.2 ha apple orchard blocks (>10-year-old) to assess the complex of generalist predators on the ground in established orchards. Each block contained 'York Imperial,' 'Stayman,' 'Golden Delicious,' 'Delicious,' and 'Empire' apple trees (M7 rootstock) planted at 4 × 5 m spacing in a completely random design in 1984. Orchard management was the same, consisting of herbicide application in the tree row, regular mowing in the alley between rows, pruning, and no insecticide use since 1989. Pitfall samples were taken from the blocks during 7 day sample periods beginning 27 June, 3 July, 10 July, 18 July, 25 July, and 1 August. Ten pitfall traps per block were randomly placed within rows of apple trees, 0.4 m from the base of a tree. To prevent rainfall entry, each trap was covered with an inverted 100 × 15 mm plastic petri dish suspended about 2 cm above the jar rim on stakes. Ethylene glycol (50 ml per trap) was added at the beginning of a 7-day-sampling period. All arthropods collected were identified to either order or family. Taxa with <20 individuals collected across the season were excluded from the analysis. Generalist predators were pooled across the six sampling periods, and the percentage contribution by taxon was calculated for the predator complex. Mean predator abundance was calculated within time period by taxon (PROC MEANS, SAS Institute, 1998).

2.2. Field study comparing ground habitat treatments

This study compared the following treatments to ground habitat for their effects on arthropod predators and prey in a new apple ('Golden Supreme' on M9 root stock) orchard: (1) 8 cm composted poultry manure mulch (Potomac Valley Conservation District, Moorefield, WV), (2) 8 cm polyester fiberfill mulch (Wellman, Fayetteville, NC), (3) herbicide-treated vegetation stubble (2.3 kg [AI]/ha paraquat applied 3 June and 13 July), and (4) bare ground control (plants \geq 2 cm high hand-removed 3 and 17 June, 1 and 20 July, 3 and 19 August, and 24 September 1998). The experimental plots (1 \times 6 m, with 5 apple trees planted in a row at 1.2 m spacing) were replicated six times in a randomized complete block. Prior to planting, all treatments received glyphosate (1.12 kg [AI]/ha) in a 5 \times 86.5 m strip to kill all plants in the tree row. Slow-release synthetic NPK fertilizer (10-10-10, 0.56 kg per tree) was applied to control, herbicide, and synthetic mulch plots on 7 May 1998, to provide nutrients comparable to those released by the composted manure mulch (Wright et al., 1998).

To measure the effect of ground habitat on the relative abundance of prey and generalist predators, pitfall trapping was conducted during seven sampling periods (5–16 June, 2–9 July, 21–28 July, 5–12 August, 18–25 August, 8–15 September, and 29 September–7 October 1998), as described above (three traps per treatment plot). All arthropods collected were identified to order or family and classified as prey, generalist predator, or other prior to analysis. Taxa with <20 individuals collected across the season were excluded from the analysis. Generalist predators were pooled across the six sampling periods, and the percentage contribution by family was calculated for the predator complex within habitat treatment. Analysis of variance was performed using log transformed variables for the number of predators and prey per plot, within time period (PROC MIXED, SAS Institute, 1998). Where treatment effect was significant, mean separation was performed by least significant difference ($P = 0.05$, SAS Institute, 1998). To test for an association between generalist predator abundance and prey availability, Spearman's rank correlation analysis was performed using pitfall trap data within habitat treatments (PROC CORR SPEARMAN, SAS Institute, 1998).

2.3. Predation of sentinel larvae

The same field plots used for pitfall sampling of arthropods were used in a split-plot experiment to measure the effect of ground habitat on biological control of codling moth larvae. The experiment was a randomized complete block split-plot design, with ground habitat as the whole-plot factor (control, herbicide, compost mulch, and synthetic mulch) and exposure to arthropod predators (+/–) as the sub-plot factor.

Predator exposure was manipulated by inclusion cages that permitted arthropod predator entry and control cages that excluded all predators. Cages (1728 cm³) were constructed of transparent mylar sides and a polyester mesh top (32 \times 32 mesh per 2.5 cm) affixed with clear silicone caulk. Predator inclusion cages were open at the bottom and were suspended 1–2 cm from the habitat surface on four stakes, enabling arthropod predators to move freely underneath. Control cages were sealed underneath with a mesh bottom affixed with silicone caulk to exclude all arthropods, and a velcro seam was added to the mesh top, enabling insertion of sentinel larvae. One inclusion and one control cage were established per plot at random locations on either side of the center tree, at a minimum distance of 1 m from one another.

Laboratory-reared codling moth larvae (fourth and fifth instar supplied by USDA, ARS, Yakima Agricultural Research Laboratory, Wapato, WA) were tethered with 5–6 cm nylon upholstery string in a double knot, 4–5 mm posterior to the head capsule (Riddick and Mills, 1994; Weseloh, 1990). Tethered larvae (4 or 5 larvae per dish) were attached to the top of a 15 \times 100 mm plastic petri dish covered with a moistened paper disc. The end of each tether was anchored to the center of the dish with Scotch tape, allowing larvae to move around the dish. On 9 and 29 July, one dish with sentinel larvae was put into each cage (predator exclusion and predator inclusion) per plot at dusk. Dishes were removed after 12–14 h, and larvae were examined microscopically for symptoms of predation by spiders, carabids, or ants earlier noted by laboratory observations (Mathews, 1999).

The sentinel prey experiment was repeated on 12 August and 25 September with human observers stationed in the plots. Dishes exposed to predators in each habitat were monitored for predator activity at 15 min intervals from dusk to 12 am, when predation was expected to be greatest. Sentinel larvae were observed with the aid of a flashlight covered with a red plastic filter, to minimize predator disturbance. Incidence of arthropod foraging on the petri dish and feeding on the larvae was recorded. For ants observed in groups of 10 or more per dish, one individual was collected in a vial for later taxonomic identification at the Systematic Entomology Laboratory (USDA–BARC, Beltsville, MD). Human observers vacated the plots at 12 am. Dishes were removed 7–8 h later and examined for signs of predation.

The percentage of larvae preyed upon per petri dish was recorded. Following arcsin transformation, data from each date were analyzed using a repeated measures ANOVA, to determine if ground habitat affected the percentage of predation of sentinel larvae (PROC MIXED, REPEATED; SAS Institute, 1998). In addition, data for all four dates were subsequently analyzed in a repeated measures ANOVA, to determine if human presence in the plots affected predator activity (PROC MIXED, REPEATED; SAS Institute, 1998).

The percentage of plots in which predator foraging or feeding were observed from dusk to 12am was calculated by individual predator group. The non-parametric Cochran test for related observations was used to test for differences in predator feeding or foraging incidence observed in the habitats (Cochran *t* test, Conover, 1971).

3. Results

3.1. Composition of generalist predator complex

Pitfall traps in the >10-year-old apple orchard captured 1780 individual ground-dwelling generalist predators in the taxa Araneae, Opiliones, Carabidae, Cicindellidae, Dermaptera, Formicidae, Geocoridae, Staphylinidae, and Coleoptera (unidentified larvae). The complex was numerically dominated by Formicidae (60% of all predators collected), Araneae (17%), Carabidae (10.3%), Opiliones (8%), and Staphylinidae (2%). Cicindellidae, Dermaptera, Geocoridae, and larval Coleoptera collectively accounted for 2.7% of the total captured. Temporal abundances for the predominant predators are presented in Table 1. Formicids dominated all sampling periods except for 18 July, when Araneae outnumbered them. Abundance of major predator groups peaked by mid-July and then declined substantially.

3.2. Prey availability and predator abundance in the habitats

The ground predator complex in the newly planted apple orchard (Fig. 1) had the same 9 taxa as the >10-year-old apple orchard (Table 1). Formicids dominated the predator complex, regardless of ground habitat treatment, accounting for 66–74% of predators collected (Fig. 1). Araneae were second in abundance in all four habitats. Staphylinidae abundance surpassed that of Carabidae in the compost mulch only. Opiliones, Der-

maptera, Cicindellidae, Geocoridae, and larval Coleoptera collectively accounted for 7% of the total predators collected in the compost mulch, 5% in the synthetic mulch, 4% in the herbicide, and 3% in the control.

Ground habitat treatment significantly affected abundance of the generalist predator complex during early and mid-season sampling periods (5–16 June: $df=3, 15, F=14.80, P<0.0001$; 21–28 July: $df=3, 15, F=7.45, P=0.003$; and 18–25 August: $df=3, 15, F=5.75, P=0.001$). Predator abundance was significantly greater in the compost mulch than in all other habitats for each of these periods ($P<0.05$, Fig. 2). Predators also reached numerically higher densities in the compost mulch than other habitat treatments during the periods of 2–9 July and 5–12 August. During peak abundance (before 28 July), predator populations in the compost mulch treatment outnumbered those of other treatments by more than twofold. The compost mulch predators declined substantially in August, but they still outnumbered predators in the other treatments. However, by mid-September, predator populations were about equal size in all treatments.

Potential prey taxa collected in pitfall traps included Acari, Collembola, Aphididae, Eriosomatidae, Thysanoptera, and larval Lepidoptera. Ground treatment significantly affected prey abundance in every sampling period (5–16 June: $df=3, 15, F=50.40, P<0.0001$; 2–9 July: $df=3, 15, F=52.06, P<0.0001$; 21–28 July: $df=3, 15, F=76.63, P<0.0001$; 5–12 August: $df=3, 15, F=32.39, P<0.0001$; 18–25 August: $df=3, 15, F=9.64, P=0.001$; 5–12 September: $df=3, 15, F=10.22, P=0.001$; and 29 September–7 October: $df=3, 15, F=19.23, P<0.0001$). Prey abundance was consistently and significantly higher in the compost mulch than in the other three habitats during every time period (LSD, $P<0.05$; Table 2). Prey were least abundant in the synthetic mulch habitat in 5 of 7 sampling periods. There was a significant, positive correlation between predator and prey abundance in the compost mulch habitat ($r=0.54, P=0.0003$).

Table 1
Temporal abundance of generalist predators in >10-year-old apple orchard by pitfall sampling, 1997

	Mean No. \pm SE individuals per trap ^a					
	27 June	3 July	10 July	18 July	25 July	1 August
Formicidae	48.8 \pm 10.0	37.9 \pm 4.0	22.7 \pm 9.9	5.8 \pm 2.1	6.4 \pm 2.3	4.9 \pm 0.9
Araneae	10.2 \pm 1.9	10.7 \pm 3.8	2.5 \pm 1.0	7.1 \pm 4.5	2.4 \pm 1.2	1.8 \pm 0.7
Carabidae	4.2 \pm 2.0	3.9 \pm 0.9	7.8 \pm 2.0	2.0 \pm 0.6	1.4 \pm 0.4	0.6 \pm 0.3
Opiliones	4.8 \pm 2.9	2.5 \pm 1.4	1.2 \pm 0.5	1.4 \pm 0.5	2.7 \pm 1.4	3.6 \pm 1.4
Staphylinidae	3.3 \pm 1.5	0.0	0.3 \pm 0.2	0.4 \pm 0.3	0.3 \pm 0.2	0.1 \pm 0.1
Dermaptera	0.0	0.7 \pm 0.5	0.2 \pm 0.1	0.0	0.0	0.0
Geocoridae	0.0	0.1 \pm 0.1	0.2 \pm 0.1	0.2 \pm 0.1	0.3 \pm 0.2	0.4 \pm 0.2
Cicindellidae	0.0	0.1 \pm 0.1	0.0	0.0	0.0	0.0
Coleoptera larvae	0.2 \pm 0.2	1.5 \pm 1.0	0.0	0.1 \pm 0.1	0.6 \pm 0.3	0.4 \pm 0.4

^a Date listed indicates beginning of 7-day continuous pitfall sampling period.

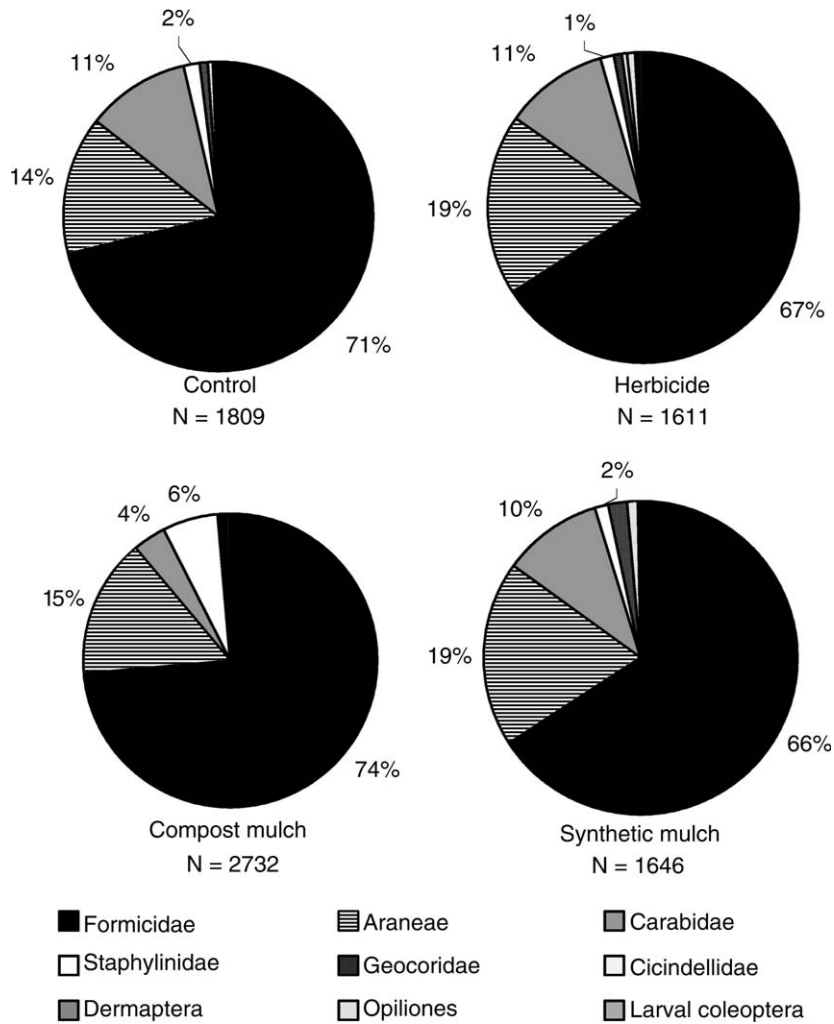


Fig. 1. Composition of the generalist predator complex in the habitat treatments of the apple orchard floor. Percentages reflect total number of individuals collected per treatment in 7 pitfall sampling periods, 1998.

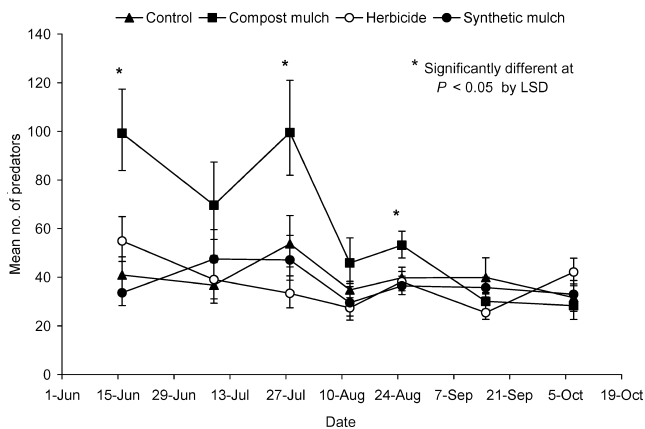


Fig. 2. Temporal abundance of generalist predators collected in the habitat treatments of the apple orchard floor. The means (±SEM) are based on three pitfall trap collections per plot during 7–10 days sampling periods, 1998.

3.3. Predation in the habitats

Ground habitat significantly affected percentage predation of sentinel codling moth larvae during mid-season, when humans were absent from the plots (9 and 29 July: $df = 3, 38, F = 3.95, P = 0.02$). Significantly more *C. pomonella* larvae were attacked in the herbicide-treated habitat (mean 81.3% predation) than in the compost mulch or synthetic mulch habitats ($P < 0.05$, LSD, Fig. 3A). Larval mortality was significantly less in the synthetic mulch (mean 33.8%) than in the control or herbicide-treated habitats ($P < 0.05$, LSD, Fig. 3A). The analysis showed no time effect for assays conducted on 9 and 29 July ($P > 0.05$). Percentage predation of *C. pomonella* did not vary significantly between ground habitats for predation assays conducted later in the season, when human observers were present in the plots

Table 2

Effect of habitat treatments to the apple orchard floor on the abundance of potential prey^a for generalist predators, 1998

	Log mean ^b No. \pm SEM prey per three pitfall traps per plot						
	5–16 June	2–9 July	21–28 July	5–12 Aug.	18–25 Aug.	5–15 Sept.	29 Sept.–7 Oct.
Compost mulch	6.8 \pm 0.2a	6.7 \pm 0.1a	7.4 \pm 0.1a	7.0 \pm 0.2a	6.5 \pm 0.2a	5.6 \pm 0.3a	5.1 \pm 0.3a
Control	5.3 \pm 0.2b	4.7 \pm 0.1b	5.1 \pm 0.1b	5.3 \pm 0.2b	5.3 \pm 0.2b	4.2 \pm 0.3b	3.9 \pm 0.3b
Herbicide	5.2 \pm 0.2b	5.0 \pm 0.1b	5.2 \pm 0.1b	5.3 \pm 0.2b	5.2 \pm 0.2b	3.9 \pm 0.3b	3.8 \pm 0.3bc
Synthetic mulch	4.0 \pm 0.2c	4.6 \pm 0.1b	4.5 \pm 0.1c	4.7 \pm 0.2c	5.5 \pm 0.2b	4.0 \pm 0.3b	3.3 \pm 0.3c

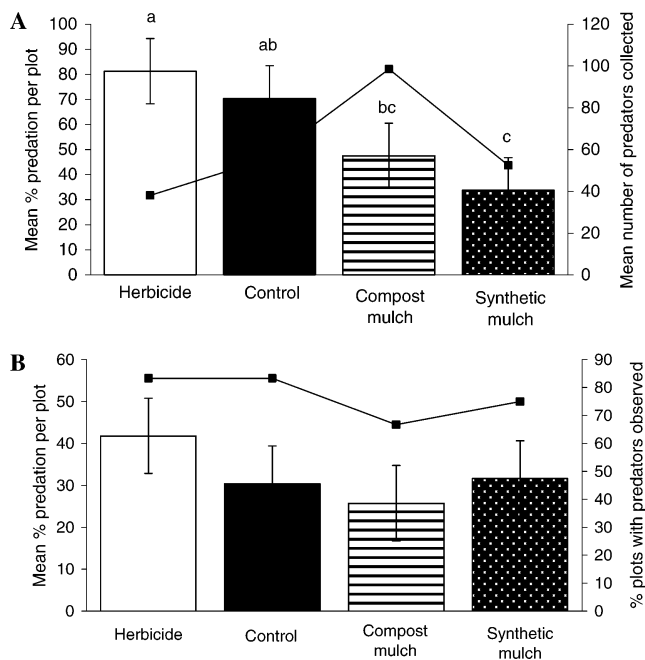
^a Prey includes Acari, Collembola, Aphididae, Eriosomatidae, Thysanoptera, and larval Lepidoptera.^b ANOVA and mean comparisons performed on log transformed data. Means sharing the same letter within columns are not significantly different at $P = 0.05$ by LSD.

Fig. 3. Nocturnal predation of sentinel codling moth larvae and predator activity in apple by habitat treatment, 1998. The bar graphs show the mean percentage (\pm SEM) of larvae attacked. (A) Assays conducted 9 and 29 July, humans absent; means sharing the same letter are not significantly different at $P = 0.05$ by LSD. The line graph represents ants and carabids collected during 7-day continuous pitfall sampling periods 2–9 July and 21–28 July. (B) Assays conducted on 12 August and 25 September with humans present from dusk to 12 am. The line graph shows the percentage of field plots with ants and carabids observed foraging or feeding upon sentinel larvae from dusk to 12 am.

Table 3

Incidence of arthropod predators observed foraging in the habitat treatments or directly feeding upon tethered *C. pomonella* larvae, 12 August and 25 September, 1998^a

Predator activity/Taxon	% plots with predators observed			
	Control	Compost mulch	Herbicide treated	Synthetic mulch
Foraging	50.0	33.3	66.7	58.3
Carabidae	33.3	8.3	41.7	33.3
Formicidae	16.7	25.0	25.0	25.0
Feeding upon larvae	50.0	75.0	83.3	50.0
Carabidae	8.3	16.7	25.0	25.0
Formicidae	41.7	58.3	58.3	25.0

^a Plots (12 replicates per habitat treatment) with sentinel prey observed from dusk to 12 am at 15 min intervals using flashlight with red filter. No significant differences among habitats were detected by t test ($P = 0.05$).

(12 August and 25 September: $P = 0.90$, Fig. 3B). However, a significant time effect occurred for the late-season assays ($df = 1, 38, P = 0.02$). Mean predation was significantly higher on 12 August (51.93%) than on 25 September (15.42%) ($P < 0.05$, LSD). Human presence in the plots affected predation of sentinel larvae ($df = 1, 86, F = 6.08, P = 0.02$). Mean predation was significantly lower when observers were present (37.92%) than without observers (58.23%) in the plots ($P < 0.05$, LSD).

Carabids and ants were the only predators observed foraging near sentinel *C. pomonella* larvae or attacking them directly during the nocturnal observations. The percentage of plots in which predation or foraging by carabids and ants was observed is shown in Table 3 and Fig. 3B. Foraging and feeding were observed in a greater percentage of herbicide-treated plots, although this difference was not significant (t test; $P > 0.05$). Ant feeding was more prevalent than carabid feeding in control, herbicide, and compost mulch (Table 3). However, foraging by carabids was observed more than foraging by ants in control, herbicide, and synthetic mulch habitats (Table 3).

Ants fed collectively, with 5 or more attacking a single sentinel larva simultaneously, while carabids exploited the prey individually. Seven ant species were observed attacking the sentinel larvae: *Aphaenogaster rudis* (Emery), *Formica nitidiventris* (Emery), *Formica subsericea* (Say), *Lasius alienus* (Foerster), *Lasius neoniger* (Emery), *Prenolepis imparis* (Say), and *Solenopsis molesta* (Say) (Det D.R. Smith, Systematic Entomology

Laboratory, USDA Beltsville Agricultural Research Center, Beltsville, MD). Carabids stopped feeding and quickly dispersed upon contact with the flashlight beam. Ants, on the other hand, did not respond to observations made with the flashlight.

4. Discussion

The apple orchards supported a diverse ground predator complex that was numerically dominated by ants, ground beetles, and spiders known to feed upon common apple pests such as aphids and codling moth larvae and pupae (Hagley and Allen, 1988; Jaynes and Marucci, 1947; Riddick and Mills, 1994; Wyss et al., 1995). The predominant predator groups were present consistently through the season, indicating that the complex maintains its general composition even when numbers decrease overall (Table 1). The ground predator complex in the newly planted apple orchard consisted of the same taxa and showed a similar temporal occurrence as that in the >10-year-old apple orchard.

Our study demonstrated that abundance of these predators can be enhanced by adding organic material to the ground habitat of an apple orchard. The results concur with the findings of previous studies involving organic soil amendments in old fields and annual cropping systems (Badejo et al., 1995; Brust, 1993; Culliney and Pimentel, 1985; Larsen et al., 1996; Morris, 1922; Riechert and Bishop, 1990). In our study, abundance of the predator complex was increased by more than 2× on average in the compost mulch habitat than all other treatments (Fig. 2). A trend of higher predator density in the compost mulch continued through the growing season until early September, when predator abundances in the four habitats were similar. The compost manure habitat consistently supported greater densities of detritivorous and fungivorous prey, compared to the other four habitats (Table 2), and predators were correlated with prey abundance in the compost mulch habitat. Yet predation of *C. pomonella* larvae was higher in the herbicide-treated habitats that consistently accommodated lower alternative prey densities (Fig. 3A, Table 2). We found significantly greater biological control levels in the herbicide-treated habitat that supported lower predator densities during the 7-day-period preceding sentinel larva introductions (based on pitfall trap sampling, Fig. 2, 9 and 28 July, and Fig. 3A). The habitat that consistently contained more predators (compost mulch) actually had significantly lower biological control rates than the herbicide-treated habitat (Figs. 2 and 3A) possibly due to predator satiation from feeding on alternative prey, predator interference, or intraguild predation. Ants and carabids, the two predator groups observed feeding upon *C. pomonella* larvae in our study, are both known to consume alternative

prey (Hengeveld, 1980; Lovei and Sunderland, 1996; Way and Khoo, 1992) and to attack other arthropod predators (Lovei and Sunderland, 1996; Stradling, 1987). In laboratory experiments, adult carabids were observed to be cannibalistic even in the presence of *C. pomonella* prey (Mathews, 1999). Snyder and Wise (1999) doubled carabid densities in vegetable plots, but were unable to attain increases in biological control due to predator interference. Researchers have also suggested that ants hold the potential to disrupt biological control through predator interference (Eubanks, 2001; Rosenheim et al., 1995).

The higher predation rates in the herbicide-treated plots may also have been related to their stubble habitat used by carabids and spiders. The herbicide-treated plots contained a melange of dead vegetation stubble that could be used for shelter from other predators and for shade cover during the day. In the laboratory, carabids were shown to forage preferentially in stubble habitat, as compared to either compost mulch or synthetic mulch (Mathews, 1999). Previous research has shown higher densities of spiders (Bogya and Marko, 1998) and carabids (Honek, 1997a; Lys, 1994) in weedy habitats versus bare ground or mowed areas. Finke and Denno (2002) demonstrated that intraguild predation was reduced for wolf spiders (*Pardosa littoralis*) and mirid bugs (*Tytthus vagus*) and predation of planthopper (*Prokelisia dolus*) prey was increased in *Spartina alterniflora* habitats with thatch added as compared to those without thatch. Comparison of predator abundance in the compost mulch versus the synthetic mulch in our study suggested that the physical habitat created by mulching was not beneficial to the predator complex. The synthetic mulch mimicked the physical structure of the compost mulch but contained significantly lower densities of detritivorous and fungivorous prey throughout the season (Table 2), as well as lower predator abundance (Fig. 2). Thus, the increase in predator densities in the compost mulch treatment was likely linked to resource abundance, rather than habitat structure.

Although the predator complex as a whole was enhanced by the application of compost mulch, individual predator taxa may have responded differentially to the habitat treatments. For instance, seasonal pitfall trap data for the four treatments (Fig. 1) suggested that carabids may not have been enhanced by the compost mulch as much as other taxa. Carabids accounted for only 4% of predators collected in compost mulch plots, but represented 11% of the total predator complex in herbicide-treated plots. Unfortunately, pitfall traps provide only a relative estimate of population density, thus precluding further inference regarding the responses of each taxon. Carabid activity can be influenced by an array of environmental factors, including temperature and habitat structure that, in turn, may

affect pitfall trap captures (Greenslade, 1964; Luff, 1975).

Our results indicate that while the presence of alternative prey in the ground habitat may be important in enhancing predator densities, the ground habitat structure may be the salient factor for reduction of *C. pomonella* prey. Our study did not investigate ground habitats that combine concentrated prey resources with physical habitat that is favorable to predators. Habitats that provide sufficient physical cover and appropriate microclimate for predators, while simultaneously supplying alternative prey, could potentially maximize biological control levels. Future work should address habitat manipulations that enhance both habitat-mediated and resource-mediated mechanisms simultaneously.

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