Intraguild predation of parasitoids by *Solenopsis invicta*: a non-disruptive interaction

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Abstract

The outcome of intraguild predation among natural enemies can have significant ramifications for herbivore suppression and biological control. Manipulating habitat complexity may alter the strength of intraguild predation, since changes in habitat complexity are often associated with concomitant changes in natural enemy abundance. Using a combination of greenhouse and field experiments, we determined if asymmetric intraguild predation by a pervasive generalist predator, the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), disrupts important parasitoids in a collard, *Brassica oleracea* L. (Brassicaceae), agroecosystem. The effect of habitat complexity on this interaction was assessed by conducting field experiments in a simple, collard monocrop and a more complex, collard-white clover intercrop. Neither the density of adult parasitoids nor the percentage parasitism of caterpillars was affected when *S. invicta* abundance was manipulated. *Solenopsis invicta* reduced the survival of the diamondback moth larvae, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) by 26% and 42% in greenhouse and field experiments, respectively, but there was no preference of *S. invicta* for parasitized or unparasitized caterpillars. An increase in habitat complexity significantly affected the abundance of both *S. invicta* and parasitoids, but had no overall effect on their interaction. The results of this study suggest that although *S. invicta* is an intraguild predator of parasitoids because it preys upon parasitized caterpillars, the action of *S. invicta* may not compromise overall biological control. This study's findings are important, because they suggest that the presence and conservation of multiple natural enemies may result in sustained pest suppression in agroecosystems, even complex systems containing many species of natural enemies including strong intraguild predators such as *S. invicta*.

Introduction

There is a growing awareness that herbivore suppression can be significantly affected by intraguild predation (predation among natural enemies that share the same prey) (Polis et al., 1989; Strauss, 1991; Rosenheim et al., 1993; Wootton, 1994; Rosenheim, 1998). In agroecosystems, the outcome of intraguild predation becomes particularly important for the biological control of economically important pests. Indeed, the most often observed outcome of intraguild predation is antagonistic and results in disrupted biological control (e.g., Rosenheim et al., 1995; Kester & Jackson, 1996; Rosenheim, 1998; Raymond et al., 2000; Eubanks, 2001;

Snyder & Ives, 2001; Eubanks et al., 2002; Kaplan & Eubanks, 2002). For example, hemipteran predators such as assassin bugs (Heteroptera: Reduviidae), damsel bugs (Homoptera: Nabidae), and big-eyed bugs (Heteroptera: Geocoridae) kill up to 90% of green lacewings (Neuroptera: Chrysopidae) in Californian cotton fields, resulting in significantly larger aphid (Homoptera: Aphididae) populations (Rosenheim et al., 1993; Rosenheim, 2001).

A few studies, however, have found intraguild interactions among natural enemies that enhance biological control (e.g., Chang, 1996; Colfer & Rosenheim, 2001). In these studies, the effect of multiple natural enemies on herbivore suppression can be additive or even synergistic. In additive interactions, the total impact of the natural enemy assemblage on a prey population is equal to the combination of the independent, individual natural enemy effects. In synergistic interactions, the behavior of one natural enemy

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increases the susceptibility of prey to a second natural enemy, and the outcome is a level of prey suppression greater than the sum of the individual natural enemy effects (Roland & Embree, 1995; Losey & Denno, 1998). With these types of interactions, enhanced biological control can occur even if intraguild predation is present. For example, Heinz & Nelson (1996) found that whitefly (Homoptera: Aleyrodidae) suppression was greatest when a generalist predator and specialist parasitoids were simultaneously released in greenhouses. The combination of natural enemies maximized whitefly control even though the generalist predator consumed significant numbers of whitefly nymphs containing parasitoid larvae. Significant intraguild predation occurred, but the interaction between the predator and the parasitoids was additive because the predator did not preferentially attack parasitized or unparasitized nymphs. This type of prey preference, along with the possibility of adult parasitoid interference, is particularly important in sustaining biological control when intraguild interactions involve parasitoids as the intraguild prey (Snyder & Ives, 2003).

The outcome (and strength) of intraguild interactions may be altered by increases in habitat complexity, an important component of agroecosystems. Increases in habitat complexity are often associated with an increase in natural enemy abundance and a possible underlying mechanism of this phenomenon is a reduction in intraguild predation (reviewed in Langelotto & Denno, 2004). For example, Finke & Denno (2002) showed that a moderate increase in habitat complexity – the presence of dead plant material in an intertidal marsh – reduced the intraguild predation of predaceous plant bugs (Heteroptera: Miridae) by wolf spiders (Araneae: Lycosidae), and consequently enhanced overall prey suppression. Although several studies from agroecosystems support the finding that increasing habitat complexity increases natural enemy abundance (Langelotto & Denno, 2004), few of these report the effect that habitat complexity has on intraguild predation per se.

The focus of this study was to characterize and assess the impact of asymmetric intraguild predation of important parasitoids by an abundant and pervasive generalist predator, the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), in a collard (*Brassica oleracea* L.) (Brassicaceae) agroecosystem. In addition, we quantified the effect of intercropping on this interaction to determine if increased habitat complexity affects intraguild predation. We addressed these questions with a combination of greenhouse and field experiments: (1) Does *S. invicta* abundance and habitat complexity affect the abundance of adult parasitoids and the parasitism of caterpillars? (2) Does *S. invicta* show a predation preference for parasitized or unparasitized caterpillars? and (3) Does habitat complexity increase or decrease *S. invicta* intraguild predation of

parasitized caterpillars? Answers to these questions will not only increase our knowledge of intraguild interactions, but could offer insight into the debate over using multiple vs. single and generalist vs. specialist natural enemies in biological control.

Materials and methods

Study system

Collards and other crucifers (*Brassica* spp.) are important green-leaf crops in the south-eastern USA (Mizelle, 1991). In this region, *S. invicta* has become one of the most abundant predators (Reagan, 1986; Vinson, 1997), and previous work in collard agroecosystems has shown that *S. invicta* may significantly reduce pest abundance and contribute to decreased collard damage and increased yield under some conditions (Harvey & Eubanks, 2004).

Solenopsis invicta, however, may negatively affect the overall biological control in a system through the intraguild predation of other beneficial arthropods (Reagan, 1986; Lee et al., 1990; Hu & Frank, 1996; Eubanks, 2001; Kaplan & Eubanks, 2002). In south-eastern cotton fields for example, *S. invicta* frequently reduce coccinellid, spider, and big-eyed bug densities by upwards of 50% (Eubanks et al., 2002). Thus, it is possible that *S. invicta* may compromise overall biological control by interfering with the natural enemies that may provide more effective control of collard pests.

The most important collard pests are diamondback moth larvae, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), and other caterpillars including *Trichoplusia ni* (Hübner) (Noctuidae) and *Pieris rapae* (L.) (Pieridae) (Endersby & Morgan, 1991; Biever et al., 1994). Parasitoids are the primary natural enemies attacking these herbivores. *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae) and *Cotesia plutellae* Kurdjumov (Hymenoptera: Braconidae) are particularly important biological control agents of *P. xylostella* (Mitchell et al., 1997a,b; Hu et al., 1998). These parasitoids can achieve parasitism rates greater than 90% and 60%, respectively (Hu et al., 1998). Given the propensity of *S. invicta* to prey upon caterpillars in this and other systems (Harvey & Eubanks, 2004), and to be intraguild predators of parasitized hosts such as aphids (Michaud, 1999; Hill & Hoy, 2003), *S. invicta* is probably a significant intraguild predator of parasitoids in collard agroecosystems.

Effect of *Solenopsis invicta* and habitat complexity on parasitoid abundance and parasitism rate

A field experiment was conducted in the spring and fall of 2001 to quantify the effect of *S. invicta* abundance and habitat complexity on the parasitism of *P. xylostella* and other caterpillars. A field site was established at the E.V. Smith Research Center, Macon County, AL. Plots (ca. 120 m^2) were planted in two habitat complexities. Ten plots were

planted as a collard monocrop (simple habitat) and 10 plots were planted as a collard-white clover intercrop (complex habitat). Clover was planted in fall 2000 to ensure a healthy stand. We attempted to minimize competition among the two crop species by planting collards early in the season prior to the clover flourishing in furrows cut into the clover plots (see Harvey & Eubanks, 2004). All plots consisted of four rows of 25 collards (45 cm within-row, 90 cm between-row spacing; Peet, 1991) and were maintained throughout each season with manual weeding.

To establish and maintain *S. invicta* abundance treatments, half the plots were treated with commercial fire ant bait (Amdro®; 0.14 g m⁻²). Amdro® is a corn grit-based bait, which is readily picked up by foraging *S. invicta*, but leaves no residue in fields and does not affect the survival of herbivores or other natural enemies (Hu & Frank, 1996; Eubanks et al., 2002; Kaplan & Eubanks, 2002). Baited plots (low *S. invicta*) were separated from control plots (high *S. invicta*) by 30 m. A previous study showed that 15 m between baited and control plots was adequate to maintain *S. invicta* abundance treatments (Harvey & Eubanks, 2004).

To quantify *S. invicta* density, pitfall traps (three per plot) were set for 24 h each week during the growing season. The pitfalls consisted of a 266 ml cup (with ca. 120 ml ethylene glycol) seated in a 90 mm PVC pipe. To quantify parasitoid density, yellow sticky cards (three per plot) were set at the same time as the pitfalls. The sticky cards (7.62 × 12.70 cm) were fastened to stakes about 90 cm above the ground.

Parasitism was estimated from field collections of caterpillars. Weekly searches of collard plants were performed during the spring and fall (2001) growing seasons. All caterpillars (species and larval instars) found on collards were returned to the laboratory and reared on an artificial diet (27 °C, L16:D8; Shelton & Collins, 2000) until adult (parasitoid or lepidopteran) emergence. In spring 2001, 50 collards per plot were searched from 22 March to 10 April. As the collards grew, searches decreased to 25 collards per plot on 19 April to 1 May, and to 20 collards per plot from 8 May to 13 June (Mitchell et al., 1997a,b). In fall 2001, 15 collards per plot were searched from 10 October to 19 November.

Predation preference of *Solenopsis invicta* for parasitized or unparasitized *Plutella xylostella* larvae

A choice experiment was conducted in the greenhouse to determine if *S. invicta* preferentially preyed upon parasitized or unparasitized *P. xylostella* larvae. A *P. xylostella* colony was established and maintained on an artificial diet following the methods of Shelton & Collins (2000). The parasitoid *Cotesia plutellae* was chosen for this experiment because of its commercial availability. Larvae were exposed to parasitoids in 3.8 l jars for 4 days. Each jar contained ca. 300 *P. xylostella* larvae (1st and 2nd instars) and 50 parasitoids (ca. 25 male,

25 female). Female *C. plutellae* can each parasitize some 300 *P. xylostella* larvae (Velasco, 1982). A ratio of 12 larvae to each female ensured successful parasitism. Parasitism was confirmed by dissecting 20 larvae from each jar: all dissected larvae were parasitized.

Individual collards were planted in 16 mosquito netting cages, 75 × 30 × 33 cm. Half of the cages were connected to 53 × 43 × 13 cm pans containing similar-sized, wild-collected *S. invicta* colonies (ca. 500 per pan) with 0.5 cm diameter plastic tubing (Eubanks et al., 2002; Kaplan & Eubanks, 2002; Harvey & Eubanks, 2004). The remaining cages were left as controls. The inside edges of the pans were coated with liquid Teflon® to prevent ant escape. *Solenopsis invicta* workers were allowed to forage in the cages for 12 h prior to infesting the plants with larvae. Five parasitized larvae and five unparasitized larvae (both types 3rd instar) were placed on each plant. Parasitized and unparasitized larvae were differentiated with a dot of differently colored, water-based paint on the thorax. Surviving larvae were counted after 9 h.

Effect of habitat complexity on *Solenopsis invicta* predation of parasitized and unparasitized *Plutella xylostella* larvae

In spring 2002, a second field experiment was conducted to determine if habitat complexity and *S. invicta* abundance were interacting to affect the *S. invicta* predation of parasitized and unparasitized *P. xylostella* larvae. Using the same field site, clover plots (planted fall 2000) and the protocol used in 2001, five plots (ca. 120 m² each) were planted as a collard monocrop and five plots were planted as a collard-white clover intercrop. The 2002 plots consisted of four rows of 15 collards. *Solenopsis invicta* treatments were established and maintained with Amdro® and abundances quantified with pitfall traps, following the same procedures and protocols as in 2001.

On three dates in spring 2002, two random collards per plot were manually cleaned of all arthropods, to remove any potentially confounding prey of *S. invicta*, and four unparasitized *P. xylostella* larvae and four larvae parasitized by *C. plutellae* (both types 3rd instar) were placed on each of these plants. Parasitized larvae were produced and differentiated following the same procedure as the choice experiment. Surviving larvae were counted at 24, 48, and 72 h.

Statistical analyses

For the first field experiment, abundance data for *S. invicta* and parasitoids were log(n + 1) transformed prior to analysis. The effects of habitat complexity and Amdro® on *S. invicta* density and the effects of *S. invicta* abundance and habitat complexity on parasitoid density were analyzed with repeated measures analysis of variance (ANOVA) (SAS Proc Mixed with repeated statement; Khattree & Naik, 1999). 'Plot' was used as the unit of replication: to

avoid pseudo-replication, data from individual pitfalls or sticky cards were averaged to obtain plot values for analysis. The effects of *S. invicta*, habitat complexity, and field season on caterpillar parasitism were analyzed with logistic regression (SAS Proc Logistic; Stokes et al., 2000).

Data from the choice experiment and the second field experiment were calculated as the proportion of parasitized larvae surviving on each plant (no. parasitized larvae/ no. total larvae). A proportion of 0.5 indicates an equal number of parasitized and unparasitized larvae and suggests no *S. invicta* preference for either larval stage. A proportion significantly less than 0.5 indicates more unparasitized larvae survived than parasitized larvae and suggests a *S. invicta* preference for parasitized larvae, and vice versa for a proportion significantly greater than 0.5. If no larvae remained on a plant, the proportion was scored as 0.5: no difference between parasitized and unparasitized larvae surviving. Proportions were arcsine-square-root transformed prior to analysis. For the choice experiment, the effect of *S. invicta* on the proportion of parasitized larvae surviving was analyzed with a one-way ANOVA (SAS Proc GLM; Cody & Smith, 1997). For the second field experiment, the effect of *S. invicta* abundance and habitat complexity on the proportion of parasitized larvae surviving was analyzed with a repeated measures ANOVA (blocked by sample date). The proportion of parasitized larvae surviving was compared to 0.5 with a t-test.

Results

Effect of *Solenopsis invicta* and habitat complexity on parasitoid abundance and parasitism rate

Solenopsis invicta *abundance.* In the spring, *S. invicta* abundance was significantly reduced by the application of Amdro®, but differences in *S. invicta* abundance between baited and control plots varied among habitats during the season (date × bait × habitat interaction; Table 1). Overall,
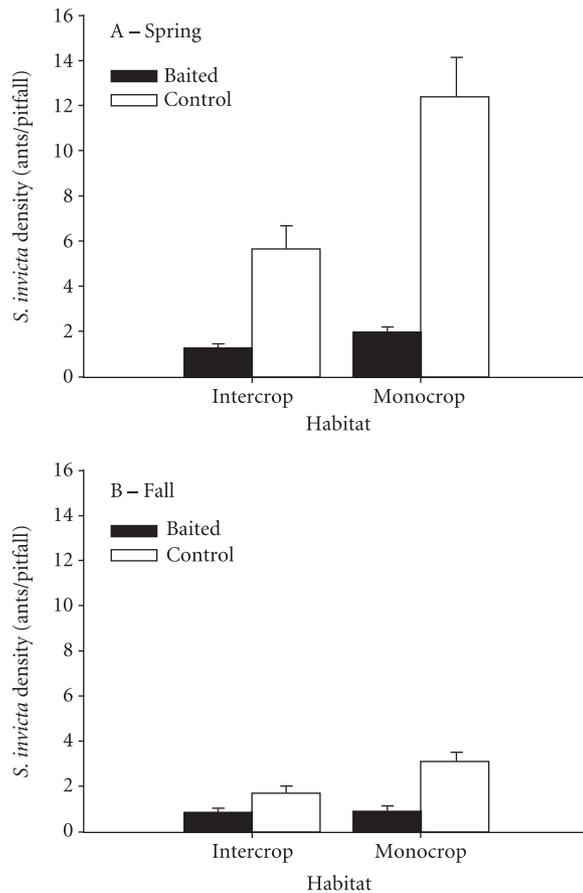

Figure 1 Mean per plot density over 24 h (+ SE) of *Solenopsis invicta* from field plots treated with Amdro®, to suppress *S. invicta* densities, and control plots from a collard-white clover intercrop and a collard monocrop for: (A) spring, and (B) fall 2001.

S. invicta were 80% less abundant in Amdro® treated plots than in control plots in both habitats, and *S. invicta* were 49% less abundant in the intercrop than in the monocrop (Figure 1A). In the fall, application of Amdro® significantly

Table 1 Repeated measures analysis of variance estimating effects of baiting and habitat complexity on the abundance of *Solenopsis invicta* in spring and fall 2001

Effect	Spring				Fall			
	Num d.f.	Den d.f.	F-value	P-value	Num d.f.	Den d.f.	F-value	P-value
Date	7	84	3.74	0.0014	5	60	18.39	<0.0001
Bait	1	12	51.28	<0.0001	1	12	22.73	0.0005
Habitat	1	12	8.36	0.0135	1	12	2.89	0.1149
Bait × habitat	1	12	0.37	0.5543	1	12	1.14	0.3067
Date × bait	7	84	1.93	0.0748	5	60	2.11	0.0765
Date × habitat	7	84	6.91	<0.0001	5	60	3.09	0.0151
Date × bait × habitat	7	84	3.45	0.0027	5	60	0.40	0.8469

Table 2 Repeated measures analysis of variance estimating effects of *Solenopsis invicta* density and habitat complexity on the abundance of *Plutella xylostella* parasitoids in spring 2001

Effect	Num d.f.	Den d.f.	F-value	P-value
Date	8	90	3.70	0.0009
S. invicta	1	12	1.10	0.3149
Habitat	1	12	40.48	<0.0001
S. invicta × habitat	1	12	0.60	0.4536
Date × *S. invicta*	8	90	0.89	0.5283
Date × habitat	8	90	2.36	0.0236
Date × *S. invicta* × habitat	7	90	1.23	0.2948

on total caterpillar parasitism in spring or fall 2001 (Wald $\chi^2 = 1.0883$, d.f. = 1, P = 0.2968). Mean parasitism over the two seasons was 61.72 ± 4.63% and 49.18 ± 3.89% in plots with suppressed *S. invicta*, and 63.72 ± 3.73% and 55.86 ± 3.75% in control plots for *P. xylostella* and total caterpillars,

and consistently reduced *S. invicta* abundance over the season (Table 1). Red imported fire ants were 62% less abundant in plots treated with Amdro® than in controls and were again less abundant (35%) in the intercrop than the monocrop (Figure 1B), but this effect varied over the season (date × habitat interaction; Table 1).

Parasitoid abundance. The most abundant caterpillar parasitoids in spring were the two *P. xylostella* parasitoids *D. insulare* and *Cotesia* spec., and unexpectedly, tachinid flies (Diptera: Tachinidae), primarily *Chetogena scutellaris* (Wulp) a highly generalist parasitoid species. The individual density of *P. xylostella* parasitoids was somewhat low, so we pooled the two species for analysis. The total density of *P. xylostella* parasitoids was unaffected by *S. invicta* abundance (Table 2, Figure 2A) and densities fluctuated between habitats over the season (date × habitat interaction; Table 2). Overall, the *P. xylostella* parasitoids were ca. 90% more abundant in the intercrop (mean density per plot ± SE; 0.16 ± 0.03 per sticky-card trap) than in the monocrop (0.02 ± 0.01 per sticky-card trap). Tachinid density was also unaffected by *S. invicta* abundance (Table 3, Figure 2B). Tachinid abundance increased significantly over the season, but their mean density was unaffected by habitat complexity (Table 3). The *P. xylostella* parasitoids were not abundant enough in fall 2001 to compare them statistically among treatments. In the fall, tachinids were ca. 60% more abundant than in spring, but their density was once again unaffected by *S. invicta* abundance (Table 3, Figure 2C). Tachinid density fluctuated between habitats during the season (date × crop interaction; Table 3), but overall, tachinids were 80% more abundant in the intercrop.

Caterpillar parasitism. Overall caterpillar densities were lower than expected in 2001 (see Harvey & Eubanks, 2004); all species including *P. xylostella* (unless otherwise indicated) were pooled for analysis. There was no effect of *S. invicta*
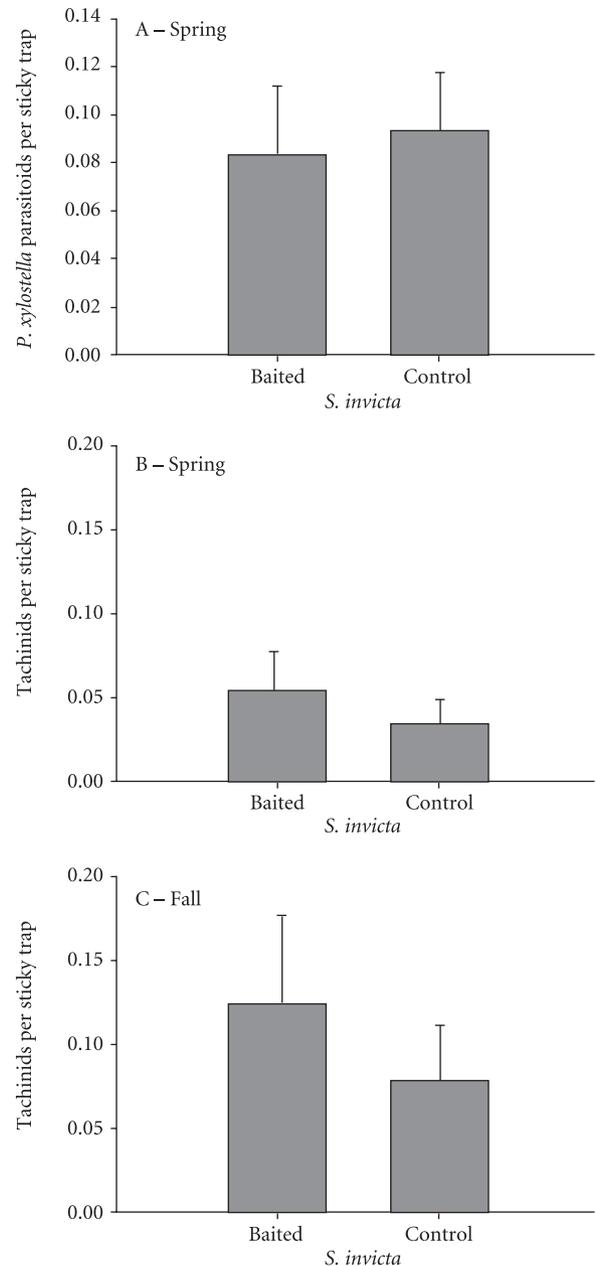

Figure 2 Mean per plot density over 24 h (+ SE) of: (A) *Plutella xylostella* parasitoids (*Diadegma insulare* and *Cotesia* spec.) in spring 2001, and tachinid flies in (B) spring, and (C) fall 2001 in plots with low (baited) and high (control) abundances of *Solenopsis invicta*.

Table 3 Repeated measures analysis of variance estimating effects of *Solenopsis invicta* density and habitat complexity on the abundance of tachinid flies in spring and fall 2001

Effect	Spring				Fall			
	Num d.f.	Den d.f.	F-value	P-value	Num d.f.	Den d.f.	F-value	P-value
Date	8	90	2.29	0.0279	5	60	1.88	0.1112
S. invicta	1	12	2.89	0.1149	1	12	0.49	0.4973
Habitat	1	12	0.80	0.3887	1	12	7.26	0.0195
S. invicta × habitat	1	12	0.14	0.7148	1	12	0.23	0.6401
Date × *S. invicta*	8	90	1.27	0.2692	5	60	1.62	0.1685
Date × habitat	8	90	0.65	0.7337	5	60	3.35	0.0098
Date × *S. invicta* × habitat	7	90	0.82	0.5732	5	60	1.68	0.1533

respectively. Percentage parasitism was significantly greater in the spring (64.75 ± 2.93%) than fall (15.76 ± 4.31%). Habitat complexity significantly affected fall parasitism, but there was no significant interaction between habitat and *S. invicta* (Wald χ^2 = 0.1097, d.f. = 1, P = 0.7405).

Predation preference of *Solenopsis invicta* for parasitized or unparasitized *Plutella xylostella* larvae

In the greenhouse, *S. invicta* reduced the survival of *P. xylostella* larvae by 26% ($F_{1,14}$ = 21.88, P = 0.0004; Figure 3A), but *S. invicta* did not show a preference between parasitized and unparasitized larvae. The proportion of parasitized larvae surviving in cages with foraging *S. invicta* (0.5) was not different from controls (0.48) ($F_{1,14}$ = 0.13, P = 0.7208; Figure 3B).

Effect of habitat complexity on *Solenopsis invicta* predation of parasitized and unparasitized *Plutella xylostella* larvae

Over the course of the experiment, the survival of *P. xylostella* larvae was 42% lower in field plots with higher *S. invicta* densities than in plots with suppressed *S. invicta* densities, ($F_{1,20}$ = 11.68, P = 0.0027; Figure 3C). The proportion of parasitized larvae surviving in plots with higher *S. invicta* densities (0.69) was greater than the proportion of parasitized larvae surviving in plots with suppressed *S. invicta* densities (0.52; $F_{1,20}$ = 6.38, P = 0.0201; Figure 3D), but the proportion of parasitized larvae surviving in high *S. invicta* density plots (0.69) was not significantly greater than 0.5 (t = −0.6776, d.f. = 71, P = 0.7499). There was no effect of habitat complexity on the survival of parasitized vs. unparasitized *P. xylostella* larvae ($F_{1,20}$ = 1.13, P = 0.3004).

Discussion

Intraguild predation from *S. invicta* could negatively affect biological control by parasitoids through interference with host-searching adults or through the predation of immature parasitoids within parasitized hosts (Lopez,

1982; Vinson & Scarborough, 1991; Hill & Hoy, 2003). The results of this study, however, suggest that *S. invicta* may not significantly interfere with the parasitoid biological control of caterpillars in collards, despite substantial intraguild predation of parasitoid larvae. This was most evident in the two-season field experiment where *S. invicta* populations were dramatically suppressed in half of the collard plots. In this experiment, neither the density of adult parasitoids (Figure 2) nor the percentage parasitism of caterpillars was significantly affected by *S. invicta* abundance. Even at the greatest *S. invicta* densities, the mean parasitism of caterpillars was nearly 60%. The greenhouse and field preference experiments also showed that *S. invicta* are unlikely to interfere with parasitoids. Foraging *S. invicta* workers were generally indiscriminant, attacking both parasitized and unparasitized caterpillars. If anything, *S. invicta* had a partial preference for unparasitized larvae in the field (Figure 3D). Overall, these results indicate a non-disruptive intraguild interaction among *S. invicta* and parasitoids, implying that predation by *S. invicta* is not likely to interfere with parasitoid biological control in this system.

These results are surprising given other studies of *S. invicta*–parasitoid interactions. Lopez (1982) found that *S. invicta* drastically reduced the populations of *Cardiochiles nigriceps* Viereck (Hymenoptera: Braconidae) by consuming parasitized pupae of the tobacco budworm, *Heliothus virescens* (Fabricius) (Lepidoptera: Noctuidae). Likewise, Vinson & Scarborough (1991) found that *S. invicta* preferentially attacked parasitized aphids. As has been observed for other generalist predators, the effects of *S. invicta* on parasitoids could be system- or species-specific, and influenced by the behavior or the development time of parasitized hosts (Chow & MacKauer, 1999; Meyhöfer & Hindayana, 2000; Meyhöfer & Klug, 2002).

In the case of the tobacco budworm, parasitism alters pupation site and lengthens the pupal stage, which likely increases the susceptibility of pupae to *S. invicta*. In our system,
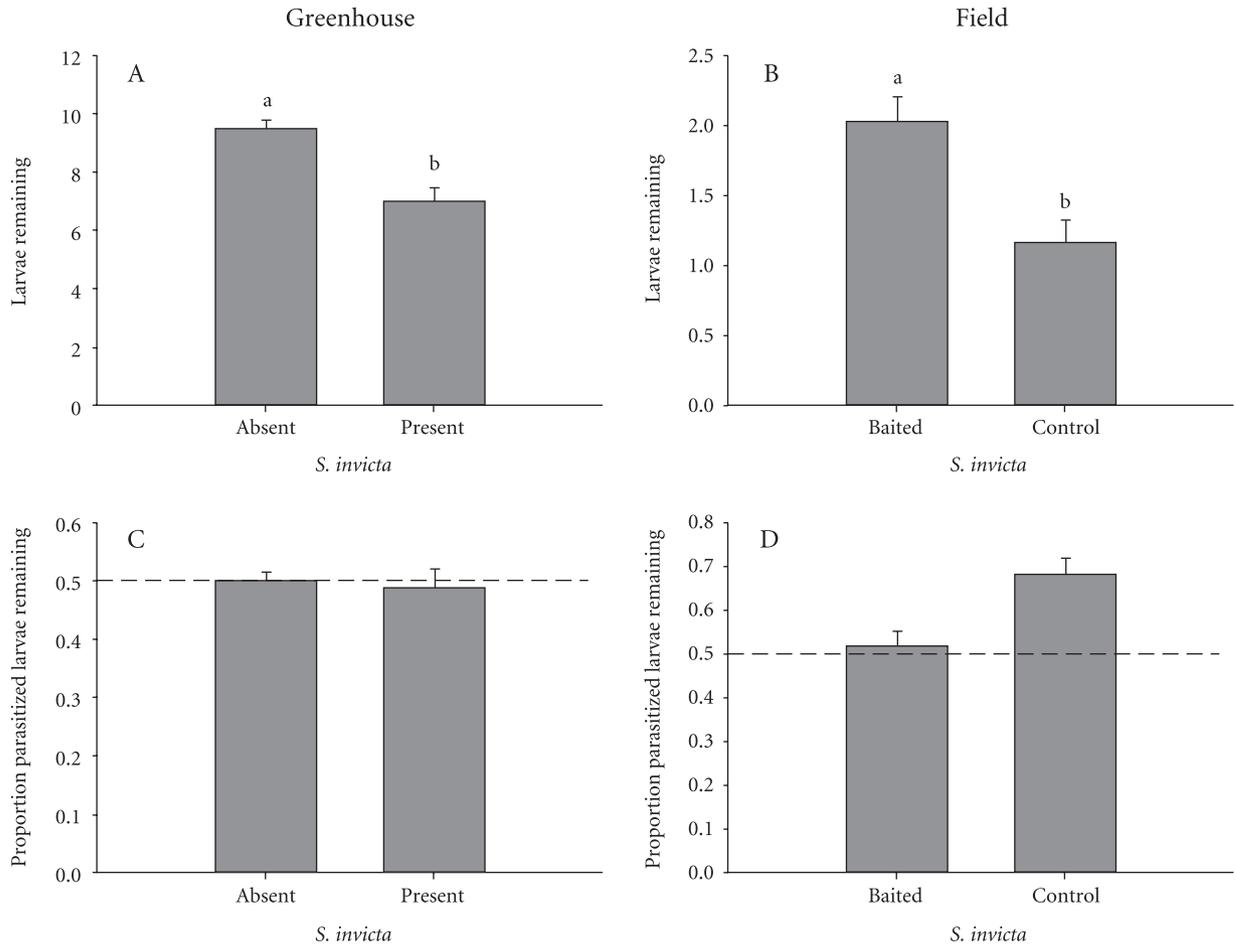
Greenhouse

Field

Figure 3 Effect of *Solenopsis invicta* on: (A, B) survival of *Plutella xylostella* larvae, and (C, D) the proportion of parasitized (by *Cotesia plutellae*) *P. xylostella* larvae surviving (no. parasitized larvae/no. total larvae) in greenhouse and field choice experiments, respectively. In the greenhouse five unparasitized and five parasitized larvae (total 10) per plant were exposed to *S. invicta* for 9 h and in the field four unparasitized and four parasitized larvae (total eight) per plant were exposed to *S. invicta* for a total of 72 h (see Results). For (C) and (D), a proportion of 0.5 indicates no difference in the number of parasitized and unparasitized larvae surviving. A proportion greater than 0.5 indicates a greater number of parasitized larvae survived than unparasitized and suggests a predation preference for *S. invicta*.

we found no evidence to indicate that *S. invicta* was preying upon *P. xylostella* or its parasitoids pupae, since both pupae were often observed on plants with actively foraging *S. invicta* workers. Unlike the tobacco budworm which pupates in the soil, both *P. xylostella* and its parasitoids pupate on the plant in a silken cocoon, which may foul worker mandibles. Furthermore, we controlled for variation in development by using only third instar larvae in both the greenhouse and field experiments. In the case of aphids, *S. invicta* are known to have mutualistic relationships with aphids that produce honeydew (Vinson & Scarborough, 1991; Kaplan & Eubanks, 2002), and parasitism dramatically reduces or stops honeydew production. As a result, *S. invicta* are likely to stop tending, and to prey upon aphids that do not produce honeydew (Brodeur & Rosenheim, 2000).

There was no evidence that an increase in habitat complexity affected the interaction between *S. invicta* and parasitoids. This may not be surprising given that there was no affect of *S. invicta* on either adult parasitoid abundance, percentage parasitism of caterpillars in the field, or the proportion of parasitized larvae surviving on collard plants (Figures 2 and 3). These results may be an artifact of adult parasitoids being able to move freely among plots with high and low densities of *S. invicta*; however, there was a significant effect of habitat complexity on both natural enemy species. This would suggest that the distances between the plots were adequate for obtaining significant results on even the highly mobile adult parasitoids. *Solenopsis invicta* was more abundant in the simple habitat, whereas parasitoids were more abundant in the more

complex habitat. These results imply there may be a balanced predation of caterpillars through the interaction of *S. invicta* and parasitoids among the two habitats, an additional, complementary benefit of the combined action of this generalist predator and the more specialized parasitoid guild.

This is one of only a few studies that have reported the occurrence of non-disruptive intraguild predation among natural enemies. There has been a long-standing debate concerning the wisdom of releasing or conserving multiple natural enemies (Heinz & Nelson, 1996; Symondson et al., 2002). Some biological control workers believe that the release or conservation of multiple natural enemies is likely to interfere with effective biological control due to antagonistic interactions among natural enemies (Turnbull & Chant, 1961; Watt, 1965; Turnbull, 1967; Ehler & Hall, 1982). Others have argued that the best biological control strategy is to release or conserve as many natural enemies as possible (van den Bosch, 1968; Huffaker et al., 1976; Heinz & Nelson, 1996). This study supports that the release or conservation of multiple natural enemies may be able to sustain high levels of pest suppression in diverse agroecosystems, even agroecosystems that contain strong intraguild predators such as *S. invicta*. Furthermore, the identification of positive interactions highlights the importance of maintaining floral and faunal biodiversity in terrestrial food webs, particularly for agroecosystems where pest management is becoming evermore dependent upon control through biological means.

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