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## Response of predators to habitat manipulation in potato fields

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## ABSTRACT

Determining the impact of habitat manipulation and predator species diversity on prey suppression is crucial in developing predictions for the impact of biological control programs. Biological control literature contains controversial evidence for the impact of increased predator species diversity and habitat manipulation on prey suppression. We investigated the individual and combined effects of two predator species (*Coleomegilla maculata* (DeGeer) and *Lebia grandis* Hentz) on the herbivore *Leptinotarsa decemlineata* (Say) in potato fields with and without rye mulch. In surveys of the endemic populations we detected that *C. maculata* is approximately 16 times more abundant than *L. grandis* and the two predator species responded in opposite manner to the habitat manipulation treatment in potato fields: on average 35% of all *C. maculata* but 85% of all *L. grandis* collected over two field seasons were found in tilled plots vs. rye mulched plots. In field cages we investigated the effect of mulching and predator identity on *L. decemlineata* suppression. Neither predator was influenced significantly by the presence of rye mulch. *L. grandis* was effective in suppressing the target prey relative to the control but *C. maculata* in the single species as well as in the two-species assemblages was not consistently able to suppress prey relative to the control. This study found no support for positive multi-predator effects since the two predator species assemblages performed as predicted based on the results from individual predators. Practical implications of this study suggest focusing conservation biological control efforts on *L. grandis* to maximize its density in *L. decemlineata* infested potato fields.

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## 1. Introduction

Agricultural habitats can be manipulated to increase predator abundance and/or diversity with the ultimate goal of achieving better biological control of pests (Root, 1973; Barbosa, 1998; Landis et al., 2000). Structurally complex habitats can increase prey survival by providing refuge from predators (Finke and Denno, 2002; Grabowski, 2004; Langellotto and Denno, 2004) and by modifying predator behavior to benefit herbivore survival (Finke and Denno, 2006). On the other hand, predator foraging efficiency may vary inversely with habitat heterogeneity, thus reducing the predators' effectiveness in prey suppression in complex habitats (Karieva, 1983; Hughes and Grabowski, 2006). Some of these conclusions are confounded by the fact that generalist and specialist natural enemies are likely to respond to habitat heterogeneity differently (Sheehan, 1986). Since predators naturally occur in assemblages in different types of habitats, it is necessary to understand the effect of habitat context on multiple predator-prey interactions. Biodiversity theory predicts that a predator assemblage will impose greater prey mortality than even the

most effective predator species alone, thus a reduction in predator species diversity leads to decreased consumption of the target trophic group (Cardinale et al., 2006 and references therein). Differences in predator species diversity can result in drastic changes in the impact of predator assemblage on pest survival (Snyder and Wise, 1999; Moran and Scheidler, 2002; Mathews et al., 2004). The identity of the species in an assemblage and the structure of a predator assemblage may play an important role in determining its effectiveness in suppressing pests. In general, the key to effective conservation biological control may be to design tactics that enhance the relative abundance of the most effective predator within the predator community (Straub and Snyder, 2006).

Crops with intensive pesticide inputs are at risk of resistance developing in key pests, and this issue has become a significant challenge in the management of numerous pest species, including the Colorado potato beetle (*Leptinotarsa decemlineata* (Say); Coleoptera: Chrysomelidae) (Whalon et al., 2008). *L. decemlineata* has several natural enemy species (Ferro, 1994), but biological control methods fail to reduce populations below economic threshold levels in conventionally managed potato fields (Ferro, 1994). The only published study to date (Brust, 1994) that examined the effect of straw mulch (i.e., structurally complex habitat) in potatoes on the natural enemy assemblage of the *L. decemlineata* reports on field observations of predators and concludes that natural enemies

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significantly reduced *L. decemlineata* populations in mulched compared to non-mulched plots.

The current study was set up to investigate the impact of habitat manipulation on two predator species alone and in combination. We began by surveying the abundance of two focal predator species of *L. decemlineata* in potato fields in order to examine their responses to rye mulch. Then we designed a field cage experiment to test the hypothesis that the identity and relative abundance of the two predator species has an effect on prey suppression. We tested this hypothesis in mulched and un-mulched potato plots. In addition, we asked the question if these treatments affected plant damage.

## 2. Materials and methods

### 2.1. Study site

Field experiments were conducted in 2006 and 2007 in Beltsville, MD, in two different fields for the 2 years, ca. 1 km apart, since potatoes were grown in rotation. The two habitat treatments were rye mulched (structurally complex) and conventionally tilled (structurally simple) potato fields. Areas of the field designated for both habitat treatments were seeded with winter rye (*Secale cereale* L., 100 kg/ha) in September 2005 and 2006 in ca. 1 ha experimental fields. In the following April of each year, before potato seeding, fields were divided into blocks (12 m by 30 m for each block). Three randomly assigned blocks were tilled to incorporate the rye stalks into the soil and another three randomly chosen blocks were left with the rye intact. Therefore, in tilled plots, potatoes were grown without mulch, but all other management methods were the same as in the rye mulched plots.

Potatoes (*Solanum tuberosum* L. 'Kennebec', 2027 kg/ha) were seeded on 27 April in 2006 and 25 April in 2007 in a 76 × 30 cm plant spacing. For the rye mulch treatment, potatoes were planted into the rye cover crop and pre-emergent herbicides (S-metolachlor at 1.78 kg AI/ha, linuron at 981 g AI/ha and paraquat dichloride at 1.71 kg AI/ha) were applied within 1 week after planting. The field was not treated with herbicides during the experiment, but low rates of insecticides (spinosad at 16 g AI/ha on 16 June 2006, and permethrin at 27 g AI/ha on 15 July 2006, and at 54 g AI/ha on 15 and 30 June 2007) for leafhopper control, and fungicide (azoxystrobin at 161 g AI/ha on 15 July 2006 and at 96 g AI/ha on 30 June 2007) were applied as needed to protect plants from severe damage.

### 2.2. Predators

The predator species studied were *Lebia grandis* Hentz, (Coleoptera: Carabidae) and *Coleomegilla maculata* (DeGeer), (Coleoptera: Coccinellidae). These two predator species were chosen because they are relatively constant members of the predator assemblage that attacks *L. decemlineata* in the eastern United States (Ferro, 1994). In addition, these two species do not feed on each other in the adult stage, therefore intraguild predation was not a source of variation. Predators were collected by hand from the same field as the *L. decemlineata* eggs, 1 day before the start of the experiment and were held in the laboratory overnight (22 ± 2 °C) with access to water.

### 2.3. Field survey

Field surveys of naturally occurring populations of the two predators were conducted in the growing seasons of 2006 and 2007. Predators were collected between 7:30 and 11:00 h from potato foliage by hand or with an aspirator. Collections lasted for 30 min in 6 by 6 m subplots once every week through the field season. We

chose this method of collection because the predators were too visually alert and highly active for conventional sampling methods (beating or quadrat sampling). Three subplots within each block were rotated weekly for these collections in order to minimize the depletion of predators from a specific part of the field.

### 2.4. Field cages

Field cages (2 × 2 × 2 m, 32 by 32 mesh Lumite screening, Bioquip, Gardena, California, USA) were set up at least 5 m from all edges of the plots, and were randomly assigned to predator treatment. The bottom edge of the cages was buried ~10 cm below the soil surface. Each cage covered eight potato plants arranged in two rows for a total of eight plants per cage. The experiment was set up on 18 June and again on 18 July 2007. After insect release, cages were assessed every 2–3 days for 2 weeks. Cages were moved and assembled over new plants located in the same field for the second time-replication. In total, 30 cages were set up twice in the summer (June and July), each time-set containing three replications of all combinations of the two factors (habitat type and predator treatments) and a control with no predators.

Prior to the set-up of cages, foliar arthropods were removed by hand searching, and by placing a yellow sticky trap (Bioquip, Gardena, California, USA) in each cage at the level of the foliage for 24 h. In addition, one pitfall trap per cage (15 cm diameter with ethylene glycol antifreeze) was kept open for 24 h to remove epigeal predators. *L. decemlineata* egg masses were collected with the leaflet they were laid on, from a nearby insecticide-free potato field, and were placed into the cages. Each egg mass was photographed prior to deployment in the cages in order to record the number of eggs per mass. Egg masses were attached to the surface of a leaf on a potato plant with a stapler. Ten egg masses were distributed by placing five masses in each of the two rows of plants within the cage. Predators were released into the cages immediately after egg masses were placed on the plants. Plant damage was visually estimated from each of the plants in the cages on June 22 and July 21, 2007.

In order to investigate the effect of predator identity on prey suppression, we used five treatments including control in a substitutive experimental design to isolate the effects of increasing species richness from increasing total predator abundance. All four predator treatments contained ten individuals per cage. Two treatments tested the predator species effects in single species assemblages, and two other treatments contained the following species combinations: 5 *L. grandis* + 5 *C. maculata* ('5 + 5') and 2 *L. grandis* + 8 *C. maculata* ('2 + 8'). We chose these combinations because they were representative of the relative abundances of the two species under field conditions. Each treatment was replicated in three blocks, each of which also had a control treatment cage containing ten egg masses without predators.

### 2.5. Statistical analyses

The numbers of predators from the field surveys were compared between the two habitat treatments with a log-linear model (Proc Genmod, link = log, distribution = Poisson, type 3 analysis). The main effects in the model were sampling date, block, mulch treatment, and predator species. We were particularly interested if the two predator species respond differently to the two types of habitats, therefore we assessed the statistical significance of mulch treatment by predator species interactions using the least-square means option ("lsmeans/pdiff" in Proc Genmod, SAS Institute Inc., Cary, North Carolina) for the 2 years separately.

We used the first two sampling dates of prey data from the cages (corresponding to the first week after predators were released in the cage) in the statistical analyses. We did this be-

cause after the first week prey were depleted. We also limited our analysis to the first week's data because the prey life stages during this time period were accessible for both predators. While *L. grandis* feeds on all life stages of *L. decemlineata*, except the adults, *C. maculata* feeds only on eggs and small larvae. During the first week after egg masses were placed into the cages, both predators could readily access the prey, and the prey life stages were combined into one variable for the analysis. The number and species of herbivores, other than *L. decemlineata*, that could not be removed from the cages before the start of the experiment were recorded during each cage sampling date. We performed the statistical analysis using these data as covariates in our model, but found no effect on the outcome; therefore we did not use them in the final analysis. *L. decemlineata* within a cage were concatenated for the statistical analysis and the proportion of prey left was transformed  $\arcsin(\sqrt{x})$  to meet the assumption of analysis of variance. Prey data was analyzed with a mixed model repeated-measures analysis of variance with sampling date, predator and mulch treatment as fixed factors, and block as random factor (Proc Mixed – covtest, spatial exponential covariance structure; SAS Institute Inc., Cary, North Carolina). Pair-wise treatment differences of means were evaluated using the Tukey adjustment for multiple comparisons with an overall 5% level of Type I error.

We calculated the per-capita impact of predator assemblages to compare the strength of *L. decemlineata* suppression among predator communities. The per-capita impact of each predator community-type was calculated using the equation:  $\ln[(N_{\text{control}} + 1)/(N_{\text{treatment}} + 1)]/P$ , where  $N$  is the number of prey and  $P$  is the number of predators in the cages (Wootton, 1997). Per-capita impact strengths were analyzed using the mixed model described above and pair-wise treatment differences of means were evaluated using the Tukey adjustment for multiple comparisons with an overall 5% level of Type I error.

Predictions for the performance of the two-species predator assemblages were calculated based on the observed performance of the single species assemblages. Based on our substitutive experimental design, predator species effects were not confounded with predator density effects; thus, the multiple predator species effects are expected to be the mean of the corresponding individual species effects, if multiple predator effects are linear (Sih et al., 1998). Departures from this average would indicate emergent non-linear effects. The predicted and observed values were compared using pre-planned contrasts (Proc Mixed, 'estimate' statement, SAS Institute Inc., Cary, North Carolina).

The percent plant damage data measured on June 22 and July 21, 2007 were transformed  $\arcsin(\sqrt{x})$  to meet assumption of analysis of variance. The effects of mulch and predator treatments on plant damage were tested separately for the two dates using a generalized linear model (Proc Glim, SAS Institute Inc., Cary, North Carolina).

### 3. Results

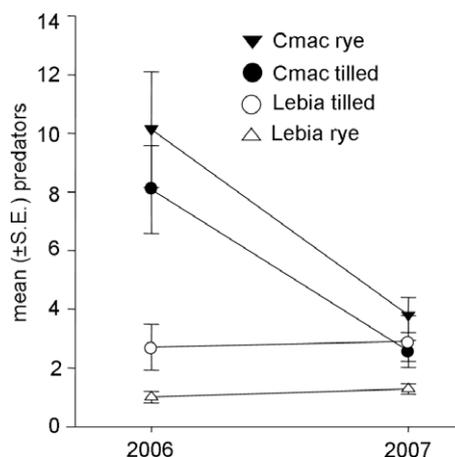
#### 3.1. Field survey

The abundance of the two predators in the field differed significantly over time (year and sampling date effects in Table 1). Regardless of habitat treatment, *C. maculata* was more abundant of the two predators, representing overall 86% of the collected specimens (Fig. 1, Table 1). Predator species responded differently to the habitat treatments (interaction term in Table 1): *C. maculata* was relatively more abundant in rye mulched plots, and *L. grandis* was more abundant in tilled plots in both years but we only found a significant effect in 2007 ( $\chi^2_1 = 5.36$ ,  $P = 0.02$ ; Fig. 1).

**Table 1**

Summary of log-linear analysis of predator (*C. maculata*, *L. grandis*) density. Weekly collections were from potato field plots in 2006 and 2007 with either rye mulch or no-mulch.

Source	d.f.	$\chi^2$	P
Year	1	5.89	0.0153
Sampling date	13	51.57	<.0001
Block	2	1.07	0.5859
Mulch treatment	1	0.51	0.4766
Predator species	1	30.21	<.0001
Mulch * predator	1	7.05	0.0079

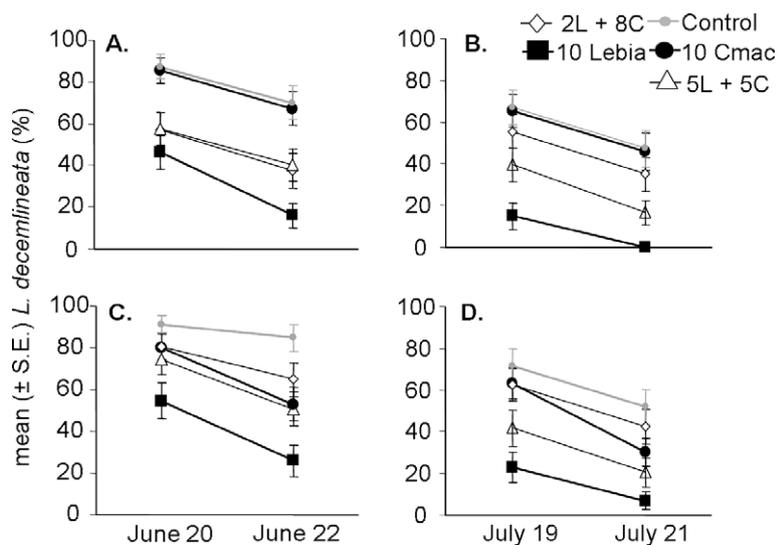


**Fig. 1.** Mean ( $\pm$ S.E.) *C. maculata* and *L. grandis* in tilled and rye mulched potato field plots in 2006 and 2007. Predators were collected from potato foliage in 6 × 6 m subplots in an experimental field in Beltsville, MD.

#### 3.2. Field cages

We found a significant effect of replication over time ( $F_{1,56} = 60.99$ ,  $P < 0.01$ ); therefore, we performed analyses separately for cages set up in June and in July. Block effect was not significant for any of the two dates ( $F_{1,27} \leq 0.64$ ,  $P > 0.05$ ). In the field cages, *L. decemlineata* abundance significantly decreased over time in June ( $F_{1,27} = 109.04$ ,  $P < 0.01$ ) as well as in July ( $F_{1,27} = 113.89$ ,  $P < 0.01$ ), with the rate of decline steeper in July (Fig. 2). Mulching did not have a significant impact on prey abundance (June:  $F_{1,27} = 1.19$ ,  $P = 0.29$ ; July:  $F_{1,27} = 0.24$ ,  $P = 0.63$ ; Fig. 2, Table 2). Prey abundance, however, was significantly affected by predator treatments (June:  $F_{1,27} = 3.88$ , July:  $F_{1,27} = 10.44$ ,  $P \leq 0.02$  for both dates) and the interaction between mulching and predator terms was not significant (June:  $F_{1,27} = 0.51$ ,  $P = 0.73$ ; July:  $F_{1,27} = 0.29$ ,  $P = 0.88$ ; Table 2), thus predator effects were consistent regardless of habitat type. Patterns of prey remaining in the cages were consistent over time across predator and mulching treatments (three-way interaction terms in Table 2). Mean *L. decemlineata* abundance in the cage with the 10 *L. grandis* assemblage was 39% less in rye and 45% less in tilled relative to the no predator control ( $t_{27} < 6.83$ ,  $P < 0.01$  for both mulch treatments and dates). The predator assemblage with 10 *C. maculata* seemed the least effective for biological control of *L. decemlineata*: on average prey abundance was 25% less in rye and 4% less in tilled compared to control treatments, but these reductions were not significant (June  $t_{27} < 1.69$ ,  $P > 0.69$  for both mulch treatments and dates).

Examining the per-capita impact of the five predator treatments in the field cages, we observed a similar pattern, with no effect of mulching (June:  $F_{1,27} = 0.11$ ,  $P = 0.74$ , July:  $F_{1,27} = 0.48$ ,  $P = 0.49$ ), a significant effect of predator treatment (June:  $F_{1,27} = 10.53$ ,  $P < 0.01$ , July: 12.73,  $P < 0.01$ ) and no interaction between predator



**Fig. 2.** Mean ( $\pm$ SE) percentage of *L. decemlineata* in field cages that were either tilled (A and B) or rye mulched (C and D), and were stocked with one of five types of predator assemblages: 10 *C. maculata* (10 Cmac), 10 *L. grandis* (10 Lebia), 2 *C. maculata* plus 8 *L. grandis* (2L + 8C), and 5 *C. maculata* plus 5 *L. grandis* (5L + 5C). Field cages were set up in June and again in July in 2007 in Beltsville, MD.

**Table 2**

Results for fixed-effects from mixed model analysis of *L. decemlineata* prey abundance on potatoes in field cages with mulch treatment (rye or no-mulch), and five predator treatments (10 *C. maculata*, 10 *L. grandis*, 5 *C. maculata* + 5 *L. grandis*, 8 *C. maculata* + 2 *L. grandis*, no predators) in June and July 2007.

Source of variation	d.f. <sup>a</sup>	F	P
<i>June</i>			
Sampling date (S)	1, 56	109.04	<0.01
Mulch treatment (M)	1, 27	1.19	0.29
Predator treatment (P)	4, 27	3.88	0.02
M * P	4, 27	0.51	0.73
S * M * P	9, 56	1.49	0.15
<i>July</i>			
Sampling date (S)	1, 56	113.89	<0.01
Mulch treatment (M)	1, 27	0.24	0.63
Predator treatment (P)	4, 27	10.44	<0.01
M * P	4, 27	0.29	0.88
S * M * P	9, 56	0.55	0.84

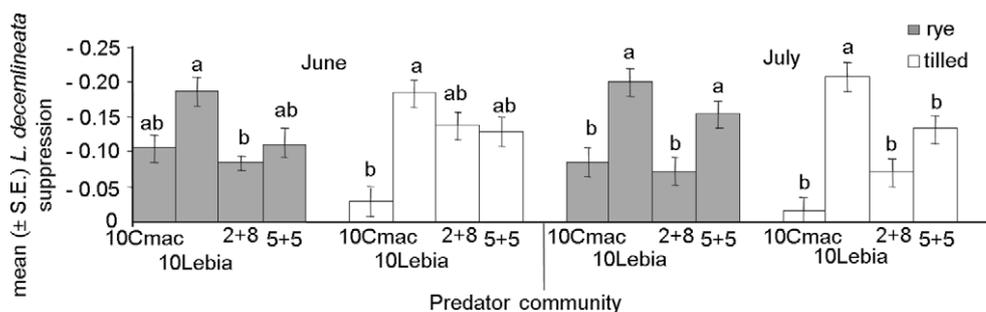
<sup>a</sup> Denominator degrees of freedom were calculated with the Kenward–Roger method.

and mulch treatments (June:  $F_{1,27} = 1.13$ ,  $P = 0.36$ , July:  $F_{1,27} = 0.36$ ,  $P = 0.83$ ). Comparing the per-capita impact of predator treatments, the 10 *L. grandis* assemblage had the highest, the two mixed species assemblages had an intermediate effect and the 10 *C. maculata*

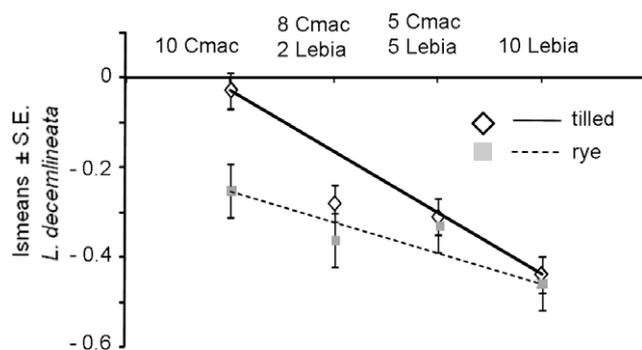
assemblage had the lowest impact on prey suppression consistently in all mulch treatments and in both time replicates (Fig. 3).

The two-species assemblages performed as expected: no significant synergistic or antagonistic effects were detected ('2 + 8' assemblage observed vs. expected:  $t_{27} = 0.16$ ,  $P = 0.87$ ; '5 + 5' assemblage observed vs. expected:  $t_{27} = 1.93$ ,  $P = 0.06$ ). Increasing the proportion of *L. grandis* in the predator assemblage enhanced the level of biological control when comparing the treatments with two-species assemblages: the assemblage with five *L. grandis* performed 1.14 times better in rye mulched and 1.04 times in tilled plots, on average, than the assemblage with two *L. grandis* (Fig. 4).

Patterns of plant damage were not consistent between the two time sets. In June rye mulched treatments received 14% more damage than tilled treatments ( $t_{21} = 2.73$ ,  $P = 0.01$ ), whereas in July tilled treatments received 17% more damage than rye mulched treatments ( $t_{21} = -5.20$ ,  $P < 0.01$ , Fig. 5). Plant damage levels compared among the predator treatments were significantly different in June ( $F_{4,21} = 4.35$ ,  $P < 0.01$ ), but were not different in July ( $F_{4,21} = 0.85$ ,  $P = 0.51$ , Table 3). In June, the impact of predator treatments on plant damage was different depending on the mulch treatment ( $F_{4,21} = 3.84$ ,  $P = 0.01$ ). In July, plant damage was significantly lower in rye mulched plots, regardless of predator treatment ( $F_{4,21} = 1.32$ ,  $P = 0.29$ , Fig. 5).



**Fig. 3.** Mean ( $\pm$ SE) *L. decemlineata* suppression by five types of *C. maculata* and *L. grandis* assemblages in field cages that were tilled or rye mulched. Per capita community impacts were calculated relative to the control treatment. Key to the predator assemblage names: 10 *C. maculata* (10 Cmac), 10 *L. grandis* (10 Lebia), 2 *C. maculata* plus 8 *L. grandis* (2 + 8), and 5 *C. maculata* plus 5 *L. grandis* (5 + 5). Field cages were set up in June (bars on the left) and again in July (bars on the right) in 2007 in Beltsville, MD. Means with the same letter are not significantly different within a set of four bars ( $t$ -test,  $P < 0.05$ ).



**Fig. 4.** Observed (symbols) and predicted (lines) least-square means  $\pm$  SE of prey suppression representing five types of predator assemblages' effectiveness in field cages with rye mulch or tilled treatments. Expected values were estimated by taking the average of the respective single species mean effects. Cmac, *C. maculata*; Lebia, *L. grandis*.

#### 4. Discussion

Understanding the relationship among habitat manipulation, predator diversity and predation rate is important in designing management tactics that improve conservation biological control strategies. Our surveys of the endemic populations of *C. maculata* and *L. grandis* indicated that the abundance of the two predator species exhibited opposite trends in the two habitat treatments, with *C. maculata* more, and *L. grandis* less abundant in rye mulched than in tilled potato plots. Based on our findings in field-cage experiments, however, we did not find substantial support that this response was a result of our habitat manipulations. Some of the potential mechanisms that may explain patterns of predator abundances observed in the field are changes in prey density and/or the presence of alternate prey. The higher abundance of *C. maculata* in the mulched field plots could theoretically compensate for its lower impact on *L. decemlineata*, but a study by Szendrei et al. (unpublished data) investigating gut analysis of predators collected from potato fields infested with *L. decemlineata* did not find support for this assumption.

Our results from the cages indicated a strong species identity effect due to increase in predation rates by the assemblage that contained the more effective predator alone. Therefore our findings support the concept that the differences in predator species abundance distributions may lead to changes in the success of biological control programs. The two-species assemblages performed as expected based on predicted values: increasing the number of the more effective predator species in the assemblage leads to increased prey suppression. With the two predator assemblages,

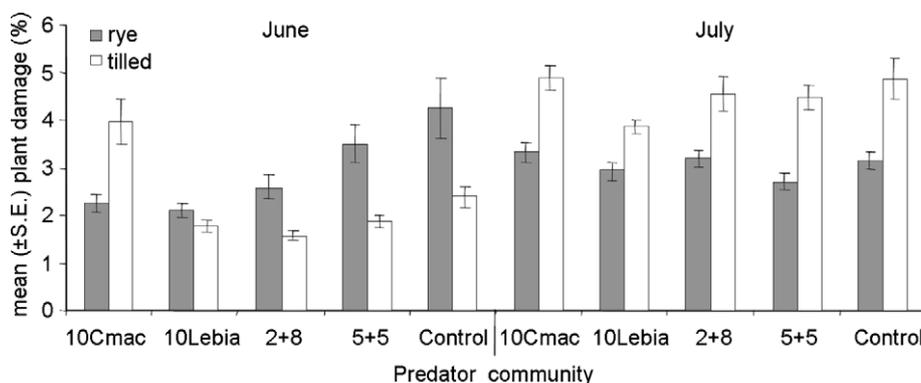
**Table 3**

Summary of analysis of variance of potato plant damage data from field cages that examined the effect of mulching (rye or no mulch), and five predator treatments (10 *C. maculata*, 10 *L. grandis*, 5 *C. maculata* + 5 *L. grandis*, 8 *C. maculata* + 2 *L. grandis*, no predators) on *L. decemlineata* in June and July 2007.

Source of variation	d.f.	MS	F	P
<b>June</b>				
Block	2	0.13	3.29	0.05
Mulch treatment (M)	1	0.20	2.92	0.09
Predator treatment (P)	4	0.46	4.35	<0.01
M * P	4	0.15	3.84	0.01
<b>July</b>				
Block	2	0.09	1.31	0.28
Mulch treatment (M)	1	0.31	25.98	<0.01
Predator treatment (P)	4	0.44	0.84	0.51
M * P	4	0.18	1.32	0.29

we found no proof of positive or negative predator diversity effects, so we conclude that in this system the two species do not interact through mechanisms such as direct or indirect behavioral interactions or resource partitioning. When extrapolating this information for the purpose of biological control on a larger scale, we need to consider that the functional benefit of predators is context dependent (Wilby et al., 2005), therefore, our findings need to be further tested in other systems.

There was a consistent, but not statistically significant, effect of habitat type on the generalist predator, *C. maculata*: in the single species assemblage, *C. maculata* eliminated more prey in the rye mulched than in the tilled treatment. We frequently observed *C. maculata* scurrying along rye stalks (Szendrei, personal observations), so the presence of stalks may have a positive behavioral or physiological effect. Field research has yielded mixed conclusions as to whether *C. maculata* contributes significantly to the biological control of *L. decemlineata* (Ferro, 1994). Our cage study and a study by Szendrei et al. (unpublished) indicate that this species does not play a significant role in *L. decemlineata* suppression. In light of the abundance of this species in our field samples, there are two puzzling questions: why are *C. maculata* more abundant in the rye mulched fields and, what is their main source of food in potato fields? These will be questions for future studies. The specialist *L. grandis* may use specific chemical cues to find its prey therefore the complex habitat structures do not interfere with its host finding. The abundance of this species in the non-mulched field plots is likely due to the greater *L. decemlineata* abundance in these types of plots (see Fig. 1; Szendrei, unpublished data). Biological control of *L. decemlineata* may be improved if a method is developed to increase *L. grandis* densities in potato fields.



**Fig. 5.** Mean percent ( $\pm$ SE) plant damage in field cages with five predator assemblages and two habitat treatments. Field cages were set up in June and again in July in 2007 in Beltsville, MD. Key to the predator assemblage names: 10 *C. maculata* (10 Cmac), 10 *L. grandis* (10 Lebia), 2 *C. maculata* and 8 *L. grandis* (2 + 8), and 5 *C. maculata* + 5 *L. grandis* (5 + 5).

Although several studies (Zehnder and Hough-Goldstein, 1990; Brust, 1994; Johnson et al., 2004) have shown reduced populations of *L. decemlineata* in potato crops with the addition of rye straw, the mechanisms of this effect are not clear. In our study, rye mulch application did not lead to better *L. decemlineata* suppression by the two tested predator species. Since our study focused exclusively on the interaction of three insect species, it is not reasonable to draw conclusions for the whole predator community in potatoes without further investigations. However, the field cage studies were based on our surveys of endemic populations of the examined predators, which is more likely to yield realistically interpretable results for biocontrol managers. Since the predator species tested herein were not affected negatively by our habitat manipulation, rye mulch could be used in potato fields for other beneficial effects such as conservation of soil moisture (Johnson et al., 2004), suppression of pest populations (Zehnder and Hough-Goldstein, 1990; Brust, 1994; Johnson et al., 2004), and potentially to encourage other natural enemy species that benefit from complex habitats.

Our cage experiment only looked at a combination of two predator species, therefore multiple combinations and levels of a diversity of predator and prey species are needed to understand the effects of increasing predator species diversity on prey suppression in more detail. According to our findings, increasing the abundance of the most effective predator in the assemblage leads to an increase in biocontrol efficiency (Landis et al., 2000; Schmitz and Suttle, 2001; Schmitz and Sokol-Hessner, 2002; Straub and Snyder, 2006) but further research will be necessary to determine whether this pattern persists when other prey and predators are present in the system.

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