Comparing the consumptive and non-consumptive effects of a native and introduced lady beetle on pea aphids (*Acyrthosiphon pisum*)

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HIGHLIGHTS

- *C. septempunctata* has a greater consumptive effect than *C. novemnotata*.
- *C. septempunctata* induced more aphid dropping behavior than *C. novemnotata*.
- *C. septempunctata* is an effective biocontrol agent but may crash *A. pisum* populations.
- The replacement of *C. novemnotata* by *C. septempunctata* may be affecting agricultural systems.

GRAPHICAL ABSTRACT
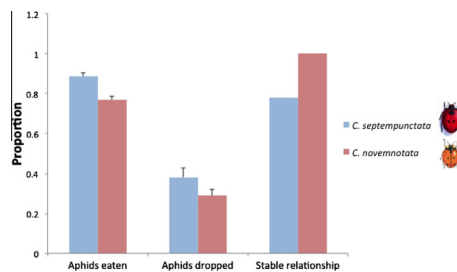
ABSTRACT

While the importation and release of foreign natural enemies in classical biological control programs can be cost-effective, the released control agent can have unintended effects, such as the displacement of native natural enemies. In this study we examined the effect of the replacement of a native coccinellid, the nine-spotted lady beetle (*Coccinella novemnotata*) by an exotic biological control agent, the seven-spotted lady beetle (*C. septempunctata*), on the ability of the coccinellid complex to control pest aphids. Specifically, we compared the consumptive and non-consumptive effect of each coccinellid species on aphids. The consumptive effect was measured by determining the functional responses for each lady beetle and calculating attack rate, handling time, and maximum feeding rate on a shared prey item, the pea aphid (*Acyrthosiphon pisum*). Non-consumptive effects were examined by assessing pea aphid dropping rates in response to foraging by the coccinellids on fava bean plants. Our results indicate that *C. septempunctata* has both a significantly greater consumptive effect and non-consumptive effect on *A. pisum* than *C. novemnotata*. Modeling indicates that *C. septempunctata* should have a greater impact on *A. pisum* populations but that its greater predatory efficiency could also lead to decreased stability in the interactions between predator and prey populations.

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1. Introduction

1.1. Background

Classical biological control, where an exotic natural enemy is imported to control a pest species, can be an effective, low-cost method for the sustained management of pest populations (Debach and Rosen, 1991; Barratt et al., 2000). Since 1888, over 700 insect biocontrol agents have been introduced into the United States (Greathead and Greathead, 1992). In California alone, major biological control projects saved over $500 million between 1900 and 1985 (Debach and Rosen, 1991). Additionally, classical biological control projects have a high benefit:cost ratio with some projects exceeding 100:1. In Australia the average estimated benefit:cost ratio of biological control projects was 10.6:1, which exceeded the ratio of chemical control projects (2.5:1) (Driesche and Bellows, 1996). Some classical biological control programs have been spectacularly successful, one example being the control

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of the cottony-cushion scale, *Icerya purchasi* Maskell by the vedalia lady beetle, *Rodolia cardinalis* Mulsant. It is estimated that this project cost less than $5000 to implement and has saved the citrus industry millions of dollars annually (Debach and Rosen, 1991).

While there are numerous examples of the successful implementation of classical biological control, there are also examples of biological control agents having an adverse impact on native flora and fauna. Stiling and Simberloff (2000) estimate that 16% of all classical biological control attempts within the United States have had a negative impact on non-target organisms.

Coccinellids are commonly used as classical biological control agents to control soft-bodied pests like aphids in agricultural systems. The seven-spotted lady beetle, *Coccinella septempunctata* L., is one of the many coccinellids that were imported into the United States for the biological control of aphids from 1957 to 1990 (Schaefer et al., 1987; Obrycki et al., 2000) and is believed to have become established in or around 1973. By 1987 the range of *C. septempunctata* had expanded to include much of the United States (Schaefer et al., 1987). *C. septempunctata* tends to be more voracious and larger than many of its native counterparts and because of this, it was expected to be an excellent biological control agent of aphids (e.g. Raak-van den Berg, 2012; Elliot et al., 1996; Gardiner et al., 2011). However, since the introduction of *C. septempunctata*, there has been a shift in the relative abundance of many native coccinellids. For instance, there has been a decline in some species such as the nine-spotted lady beetle, *Coccinella novemnotata* Herbst, the two-spotted lady beetle, *Adalia bipunctata* L., and the transverse lady beetle, *Coccinella transversoguttata* F., (Elliot et al., 1996; Obrycki et al., 2000), while other species, such as the spotted lady beetle, *Coleomegilla maculata* De Geer, have become more common.

C. novemnotata is a species of particular interest because it is a congeneric species of *C. septempunctata* and they are thought to occupy the same ecological niche (Losey et al., 2012; Harmon et al., 2007). Prior to the establishment of *C. septempunctata*, *C. novemnotata* was one of the most commonly collected coccinellids in the United States (Gordon, 1985) and was widespread across the United States (Wheeler and Hoebeke, 1995; Harmon et al., 2007). It has been proposed that its disappearance could be due to displacement by *C. septempunctata* (Wheeler and Hoebeke, 1995; Losey et al., 2012), although it is also possible that *C. novemnotata* declined for other reasons and then *C. septempunctata* expanded to fill the empty niche. Regardless of whether *C. septempunctata* is a "driver" of community change or a "passenger" (Didham et al., 2005), its replacement of *C. novemnotata* as one of the prominent natural enemies of aphids in the United States could change how the coccinellid complex interacts with aphids, which would impact biological control in agricultural systems.

The effect of a biological control agent on its prey can be assessed in terms of consumptive and non-consumptive effects. Consumptive effects occur when a predator feeds directly upon a prey item. Non-consumptive effects are those that reduce prey fitness, unrelated to death by consumption. Some of these effects include prey defensive and behavioral responses (Fill et al., 2012). Often, the non-consumptive effects that natural enemies inflict on prey populations can cause an equal or greater loss of fitness than the consumptive effects (Fill et al., 2012; Preisser et al., 2005). In the coccinellid–aphid system, the consumptive effect on aphids would be the direct consumption of the aphids. A non-consumptive effect would be the modification of aphid behavior in any way that affects its fitness. For instance, many studies have demonstrated that coccinellids and other aphidophagous predators can elicit a dropping response in the pea aphid, *Acyrthosiphon pisum* Harris, where the aphids fall from the plant to avoid predation (Evans, 1976; Roitberg and Myers, 1977; Roitberg et al., 1979; Losey and Denno, 1998). Dropping is the most common escape mechanism employed

by *A. pisum* (e.g. Montgomery and Nault, 1977). However, their propensity to drop is affected by a variety of factors such as temperature, humidity, aphid density, and the size the predator (Dixon, 1958; Brodsky and Barlow, 1986; Losey and Denno, 1998; Evans, 1976). While dropping behavior is an effective method for avoiding aphidophagous predators, under certain conditions, such as very warm, dry weather, dropping behavior can be costly and result in high aphid mortality (Roitberg and Myers, 1997; Ruth et al., 1975).

In this study we compared the consumptive and non-consumptive effects of *C. novemnotata* and *C. septempunctata* in order to gain insight into how the replacement of a native coccinellid by an exotic species will impact aphid populations. The consumptive effect was determined for both lady beetle species by determining their functional response, which is the relationship between resource density and consumption rate. It has been proposed that functional responses can be used as a means of comparing the relative impacts of invasive and native species on a prey population (Bollache et al., 2008; Dick et al., 2013). Other sources caution that several factors in the field add complexity and can cause predictions based on laboratory-based functional response studies to be inaccurate (Lester and Harmsen, 2002). Predation rates in the field are difficult to measure so there are few comparisons of laboratory and field-based rates, but one surrogate for predation rate in the field is predator distribution, as optimal foraging theory would predict that predators should concentrate their efforts on prey that offer the highest nutritional value (Roger et al., 2001). Finlayson et al. (2010) found that their laboratory predation rates accurately predicted presence and density associated with various aphid species in the field. This provides evidence that, at least for coccinellids, predation rates measured in the laboratory do reflect patterns in the field.

The non-consumptive impact of each species was determined by observing *A. pisum* dropping rates in response to the presence of adult coccinellids of both species. Due to the potential negative consequences of dropping behavior on aphid fitness (Roitberg and Myers, 1997; Ruth et al., 1975), the non-consumptive effects of each coccinellid species has the potential to further differentiate their relative impacts on aphid populations.

1.2. Objectives

Although the "replacement" of *C. novemnotata* by *C. septempunctata* has been evident for decades, *C. novemnotata* had become so rare that it was not possible to conduct a full comparison of its impact on *A. pisum* with the impact of *C. septempunctata*. Recently, through the efforts of volunteers in the Lost Ladybug Project (www.lostladybug.org), stable populations of *C. novemnotata* have been identified and laboratory colonies have been established making a full comparison possible. We initiated this study to help provide insight into how replacement of *C. novemnotata* by an exotic congeneric species, *C. septempunctata*, would affect aphid populations in agricultural systems.

2. Methods

2.1. Rearing methods and origin of lady beetles

Adult *C. septempunctata* and *C. novemnotata* were collected from Oregon in the summer of 2012 to start laboratory colonies. An additional *C. novemnotata* colony was started in 2012 from adults collected on Long Island, New York. Adult beetles and larvae were maintained separately in 44 mL plastic cups that contained a single piece of paper towel (6×2 cm) to serve as cover. Beetles were provided an *ad libitum* diet of mixed-aged *A. pisum* that had been

produced on fava bean (*Vicia faba* L.) plants. Old and dead aphids were removed from cups daily and the paper towel replaced every 2–3 days. The rearing room was kept at 23 ± 2 °C with a 16:8 (L:D) light cycle. A more detailed description of the rearing process can be found in Losey et al. (2012).

2.2. Consumptive effect test

To compare the consumptive effect of *C. septempunctata* and *C. novemnotata* populations on aphids, we conducted a study to determine their functional response. Individual adult virgin beetles (mean ± SE day old adults: 12.6 ± 0.40 days) in 44 mL plastic cups were provided a range of aphid densities, the range of which differed by species. Both male and female lady beetles were tested. *C. septempunctata* were provided 10, 15, 20, 25, 30, 35, or 40 third or fourth instar aphids and *C. novemnotata* were provided 10, 15, 20, 25, and 30 aphids. Preliminary tests indicated that adult *C. novemnotata* and *C. septempunctata* did not consume more than 30 and 40 third-instar aphids per day, respectively. These densities were chosen as the upper limit for the number of aphids provided beetles per day in our trial. The aphid density is expressed as aphid level per 44 mL.

Prior to the start of each trial adult lady beetles were sexed, weighed and then starved for 24 h. Beetles were maintained singly in 44 mL cups in an incubator at 23.3 °C ± 0.05 and 42.2% ± 0.28 relative humidity. The following day aphids were added to each cup along with a 2 × 5 cm paper towel and 100 μL of tap water. Five to six holes were poked into the cap with a metal probe to minimize condensation. This amount of water and ventilation greatly improved the survivorship of aphids as compared to our preliminary trials. After 24 h, the number of surviving, attacked, and dead aphids were counted. Any aphid that was still alive but had been attacked (as determined by melanization or noticeable bites) was put into one of two categories: (1) attacked – any aphid still alive with its head and at least 70% of its former body mass intact; insects within this category were alive and active, (2) moribund – any aphid still moving, but missing its head, or more than 30% of its body; these insects were usually lethargic or inert, discolored, and showing clear signs of poor health. Aphids within the first category could potentially reproduce or harm the plant, while aphids within the second category were assumed to be dying or to have lost their reproductive capacity. Aphids that appeared dead but were neither eaten nor attacked were counted and were assumed to have died from natural causes. These aphids tended to be immobile and discolored. The number of aphids consumed in each trial was determined by subtracting the number of surviving aphids from the total amount offered in that trial. Aphids in the attacked category were counted as surviving aphids while aphids in the moribund category were counted as consumed. An additional set of two control cups without coccinellids were set up identically to those containing beetles to measure background mortality at each aphid density tested. Between 14 and 29 replicate cups of each aphid density and coccinellid treatment were monitored over a 3-month period.

We found no significant differences between the weights or aphid consumption of the two *C. novemnotata* populations therefore we pooled the data (*P* = 0.582).

2.2.1. Analysis of the consumptive effect

The functional response of each lady beetle species was generated using R Version 2.15.2012-10-21 (R Core Team, 2012) with aphid density as our dependent variable and the number of aphids killed as our response variable. To test whether each coccinellid species was displaying a Type II or Type III functional response, we used a logistic regression to test for a negative linear coefficient. Due to the 100% consumption rates displayed by

C. septempunctata at lower aphid densities, the initial functional response approximated a Type III curve. To correct for this, we excluded the 10 and 15 aphid levels from *C. septempunctata*, which changed it into a Type II functional response. This was necessary in order to compare the two species using the Roger's equation for prey depletion (Bolker, 2008).

Our experiment yielded a single value for the attack rate (*a*), handling time (*h*), and maximum estimated feeding rate ($1/hT$) for each coccinellid species, which were calculated using the Roger's equation for prey depletion as described in Bolker (2008). The general approach to our analysis, with minor modifications, was similar to that outlined in Dick et al. (2013). Bootstrapping was used to generate additional estimates (*n* = 50) for attack rate, handling time, and maximum feeding rate, so that they could be compared using a Student's *t* test, which was performed with JMP Pro version 10 (SAS Institute, 2013; Dick et al., 2013).

Using the bootstrapped values for attack rate and handling time, the efficacy of each coccinellid as a biological control agent was quantified by estimating the *q*-value (the ratio of the equilibrium prey population with and without a predator population present (Beddington et al., (1978)) using a simulation model constructed by Sharov (Last accessed: November 2014). Additional values needed to calculate the *q*-value were: the carrying capacity of the prey population (20, estimated from the number of aphids that would fit on the length of stem in a 44 mL cup), the carrying capacity of the predator population per aphid per day (0.03 for both *C. septempunctata* and *C. novemnotata*, derived using unpublished data from Kopco) and the growth rates for both the *A. pisum* and the coccinellids (0.38 and 0.2 respectively, using data from Legrand and Barbosa (2000) and ElHag and Zaitoon (1996)). Coccinellid growth rates were calculated using the formula: $r_m = (\ln(R_0))/T$, with R_0 being the replacement rate per generation, and *T* being the mean period require for progeny production (Wyatt and White, 1977; Rodriguez-Saona and Miller, 1995; Legrand and Barbosa, 2000). The values for R_0 and *T* were taken from ElHag and Zaitoon (1996) for *C. septempunctata* and *C. novemnotata*. Additional *q*-values were generated via bootstrapping (*n* = 50), and were then compared using a Student's *t* test.

To ensure coccinellid sex ratios were not unbalanced, we performed a chi-square test using R Version 2.15.2012-10-21 (R Core Team, 2012). This was necessary due to the differential aphid consumption rate of each sex.

We found no significant differences between the weights or aphid consumption of the two *C. novemnotata* populations (*P* = 0.582) and therefore pooled the data.

2.3. Non-consumptive effect

Aphid dropping behavior in response to the presence of an adult coccinellid was monitored to estimate the impact of *C. novemnotata* and *C. septempunctata* on this non-consumptive effect. One-week old *V. faba* seedlings were transplanted into inverted 237 mL funnels filled with Lambert soil (Quebec City, Canada) LM-series professional growing media. The base of this structure was sealed with a 100 × 15 mm petri dish that was held in place with Parafilm (Pechiney Plastic Packaging Company, Chicago, Illinois).

A diagram of the apparatus used for testing the non-consumptive effects of lady beetle on aphids can be viewed in Fig. 1. A ring stand was mounted with two rings. After 4–5 days of additional growth the funnels containing plants were placed onto the top ring of the ring stand. The bottom ring was outfitted with a 1.89 L funnel that was coated with Insect-a-Slip (BioQuip, Rancho Dominguez, CA) to prevent aphids that dropped from the plant from climbing out. Additionally, a 4 cm diameter plastic mesh circle (hole size 3 × 3 mm) was placed at the funnel exit that allowed

Fig. 1. (a and b) The experimental set up for the dropping experiment. (1b) The platform used to place *A. pisum* on the plant.
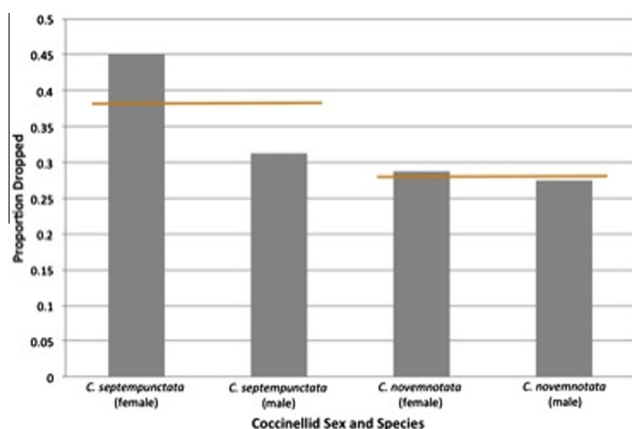

Fig. 2. The Proportion of *A. pisum* dropped relative to coccinellid sex (Female or Male) and species (C7 = *C. septempunctata*; C9 = *C. novemnotata*). The line between the species treatments is the average of the proportion dropped between the two sexes (0.385 for C7, 0.275 for C9).

aphids to pass through the holes but prevented coccinellids from falling through. Below the 1.89 L funnel was a 125 mL Erlenmeyre flask with 25 mL of soapy water that caught. The entire apparatus was housed within a fine wire mesh cage.

Prior to the experiment, the opening from which the stem of the plant emerged from the inverted funnel was sealed with parafilm to prevent aphids from traveling down into the funnel. Then an aphid platform (Fig. 1b) was constructed by applying Insect-a-Slip to the inside walls of 44.4 mL cups. Using a heated cork borer, a 16 mm (diameter) hole was burned into the center of each cup, which was then cut once radially and placed around the stem of the plant. Cotton was wrapped around the base of the stem to further plug the hole and prevent aphids from escaping out of the bottom of the cup. The radial cut in the cups, were then taped shut to keep it in place.

Twenty-four hours prior to the introduction of lady beetles into cages, 50 third or fourth-instar aphids were placed into each platform and were allowed to climb onto the plant. The following day, the number of aphids that had died within each platform was recorded, the platforms were removed and the number of aphids that had fallen off of the plant and into the soapy water was recorded. By recording these numbers it was possible to calculate the number of aphids that remained on the plant prior to the introduction of lady beetles. One adult lady beetle (either *C. novemnotata* or *C. septempunctata*), that had been sexed, starved for 24 h to ensure maximum voracity and subsequently weighed, was added to the base of the plant using a small paintbrush. The beetles were

removed 3 h post-introduction into the cages and the number of newly fallen aphids was recorded. The experiment was conducted in a greenhouse that was maintained at 22.7 °C ± 0.73 with 41.7% ± 4.68 relative humidity.

2.3.1. Analysis of the non-consumptive effect

The effect of coccinellid species on *A. pisum* dropping behavior was analyzed with logistic regression using the statistical package JMP Pro 10 (SAS Institute, 2013). The number of aphids "dropped" and "not dropped" were counted for each replicate plant. To simulate the effect of dropping on a population basis (as opposed to an individual plant basis) the total number of aphids that "dropped" and "not dropped", across all replicates, was used for the logistic regression.

3. Results

3.1. Consumptive effect test

C. septempunctata consumed significantly more aphids at each density than *C. novemnotata* (Fig. 3). Consumption rates were significantly affected by both aphid density ($x^2 = 371.25$, $P < 0.0001$) and species ($x^2 = 247.96$, $P < 0.0001$), and there was no interaction between aphid density and lady beetle species ($x^2 = 0.73$, $P = 0.73$).

C. septempunctata exhibited a significantly higher attack rate than *C. novemnotata* ($t = 9.41$, $P < 0.0001$), and a lower handling time ($t = -19.58$, $P < 0.0001$). Additionally, *C. septempunctata* had a higher estimated maximum feeding rate than *C. novemnotata* ($t = 15.82$, $P < 0.001$). *C. septempunctata* displayed a significantly lower q-value than *C. novemnotata* (Table 1) ($t = -14.19$, $P < 0.0001$).

3.2. Non-consumptive effect test

C. septempunctata induced higher *A. pisum* dropping rates than *C. novemnotata* (Fig. 2). Aphid dropping rates were affected by both sex ($x^2 = 24.93$, $P < 0.0001$) and species ($x^2 = 18.01$, $P < 0.0001$), however, the interaction between the two was not significant ($x^2 = 3.66$, $P = 0.056$).

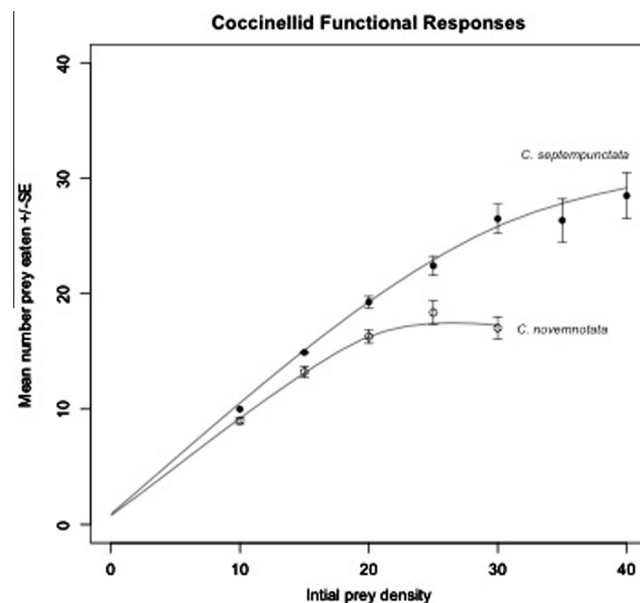**Fig. 3.** The functional responses of *C. septempunctata* and *C. novemnotata* on *A. pisum*, with the mean values and standard error.

Table 1
Functional response parameters of *C. septempunctata* and *C. novemnotata* with *A. pisum*.

Metric	Predator species		*t*	*P*
	C. septempunctata	*C. novemnotata*		
lc	−0.106	−0.101	–	Both <.001
a	8.37 ± 0.35	4.91 ± 0.10	9.41	<0.0001
h	0.03 ± 0.0005	0.043 ± 0.0004	−19.58	<0.0001
$1/hT$	33.74 ± 0.59	23.54 ± 0.26	15.82	<0.0001
q	0.066 ± 0.0024	0.106 ± 0.0016	−14.19	<0.0001

4. Discussion

Our results show that *C. septempunctata* had both a higher predatory efficiency and it elicited a stronger dropping response in *A. pisum* populations as compared to *C. novemnotata*. These results provide evidence that the replacement of *C. novemnotata* by *C. septempunctata* within the coccinellid complex could result in increased consumptive and non-consumptive pressure on *A. pisum* populations.

Changes like this are potentially important because coccinellid communities usually consist of a few dominant species. Often, just two to four species represent 90% of the individuals within a system (Hodek and Honek, 1996). Until recently, *C. novemnotata* was one of the most common coccinellids north of Mexico (Gordon, 1985) and a key player in the coccinellid complex. It is unclear whether or not the congeneric *C. septempunctata* is directly responsible for the decline in *C. novemnotata* (Harmon et al., 2007), but since its establishment between 1970 and 1980, *C. septempunctata* has rapidly spread across the United States (Wheeler and Hoebeke, 1995; Obrycki et al., 2000). Fothergill and Tindall (2010) state that *C. novemnotata* populations were declining in Missouri years before *C. septempunctata* had arrived, and conclude that it is unlikely that *C. septempunctata* is responsible for the decline. However, it is possible that *C. septempunctata* was present in Missouri and was impacting native species years before it was detected (Losey et al., 2012). *C. septempunctata* which has been described as voracious, polyphagous, and aggressive (Wheeler and Hoebeke, 1995; Gordon, 1985) has been observed preying on other predators from the same guild such as lacewings (Sengonca and Frings, 1985) and other coccinellid larvae (Raak-van den Berg, 2012) in laboratory studies. In interactions with various other native coccinellids, such as *A. bipunctata* (Raak-van den Berg, 2012) and *C. novemnotata* (Turnipseed et al., unpublished data) *C. septempunctata* tended to dominate. While many native coccinellids have decreased in abundance since the introduction of *C. septempunctata*, other species such as *C. maculata* have become more common (Elliot et al., 1996; Obrycki et al., 2000). Even if *C. septempunctata* is not causing the decline of *C. novemnotata*, there is evidence that its presence has changed the makeup of the coccinellid complex in the United States (e.g. Elliot et al., 1996; Evans, 1991; Harmon et al., 2007; Obrycki et al., 2000). Based on our results, this change in the relative abundance of different coccinellid species within the ecosystem could cause a corresponding change in the ability of the coccinellid complex to control pest populations.

It is difficult to predict how the changing densities of coccinellid species will affect agricultural and natural systems. One method that is used to predict the negative impact an invasive species might have on native communities is the comparison of functional responses between the exotic species and a functionally similar native species. Specifically, elements of predatory efficiency such as attack rate (*a*), handling time (*h*), and maximum feeding rate ($1/hT$) can be used as a gauge of relative impact on prey populations with higher values of *a* and $1/hT$ and lower values of *h* indicating a greater ecological impact (Bollache et al., 2008; Dick et al., 2013). The functional responses generated for this manuscript suggest that the proliferation of *C. septempunctata* could have a large impact on aphid, and consequently, native coccinellid communities. Breaking down the functional response into its component elements measured in this experiment give some additional insight into how *C. septempunctata* spread so rapidly and replaced the once common *C. novemnotata*.

While functional responses have been proposed as a method of predicting the impact exotic species could have on native communities, there are factors that can affect the accuracy of this method. Kestrup et al. (2011) demonstrated that in amphipod systems, intraguild predation and the environment are important factors to consider. In their experiment, they found that, while the one amphipod species had lower predatory efficiency under certain aquatic conditions, it became dominant in intraguild predation events. These events allowed the amphipod to persist even though it consistently had a lower functional response then other amphipod species. In the coccinellid–aphid complex, not only does *C. septempunctata* have a higher functional response than *C. novemnotata*, it also dominates in intraguild predation events (Turnipseed, unpublished data). Under such conditions, it would be understandable if *C. novemnotata* populations were displaced by *C. septempunctata*, especially due to the similarity of their ecological niches (Harmon et al., 2007).

It is unclear whether or not the displacement of *C. novemnotata* by *C. septempunctata* would lead to greater suppression of aphid pests. The *q*-value can be used to quantify a predator's efficacy as a biological control agent (Beddington et al., 1978). A *q*-value that is less than 0.5 is often indicative of successful biological control (Beddington et al., 1978; Sharov, n.d). Our data suggest that, both *C. novemnotata* and *C. septempunctata* are effective biological control agents. However, the lower *q*-value of *C. septempunctata* indicates that it may be a more efficient control agent then *C. novemnotata*. Interestingly, *C. septempunctata* was so effective it completely eliminated the aphid population 20% of time during our bootstrapped simulations, while *C. novemnotata* never drove the prey to local extinction. This could be due to the small space of the arena, which was used to calculate the model and the fact that no organisms can enter or leave the space. However, if this pattern holds true outside laboratory studies, it would indicate that, while *C. septempunctata* is very effective for biological control, its relationship with *A. pisum* is unstable. Conversely, *C. novemnotata* may be less effective as a control agent than *C. septempunctata*, but because it never completely eliminates *A. pisum*, it may have a more stable relationship with its prey population.

Additional evidence for the higher efficacy of *C. septempunctata* as a biological control agent was provided by our analysis of the dropping response of *A. pisum,* which was found to be greater in the presence of *C. septempunctata* than with *C. novemnotata*. However, even with the clear difference in the pea aphid's dropping response to the two predators, determining the impact of higher dropping rates on pea aphid population dynamics can be complex. The effectiveness of aphid dropping as an escape mechanism varies. In warm, dry climates dropping can result in high mortality (Ruth et al., 1975; Roitberg and Myers, 1997), reducing its efficacy of the escape mechanism. However, under other circumstances, where the predator:aphid size ratio is large, dropping can be more beneficial then remaining on the plant (Evans, 1976). When confronted by a predator, aphids can choose to run, kick, or drop from the plant (Dixon, 1958; Evans, 1976). A study by Evans (1976) demonstrated that, when *A. pisum* encounters a predator of equal or greater size (e.g. *Anthocoris nemorum* L.), running and pulling away became less successful in deterring predators. Because of this, dropping was the only option. Additionally, an experiment by Dixon (1958) showed this trend in coccinellid systems with the aphid, *Microlophium evansi* Theobald, where larger coccinellid

larvae induced higher aphid dropping rates. This pattern held true for our system as well, with the larger *C. septempunctata* triggering a greater dropping response than *C. novemnotata.* Although the optimal defensive response to a given predator can vary, the greater danger facing an aphid that remains on a plant where *C. septempunctata* is foraging coupled with the ostensibly equal rates of mortality if they do drop, indicate that a higher proportion of aphids will be killed either through consumption on the plant or alternate mortality sources (e.g. desiccation, consumption) off the plant. Thus, we predict that the overall impact of *C. septempunctata* on pea aphid populations will be substantially greater than that of *C. novemnotata*, the species it has replaced.

Beyond suppressing aphid populations, dropping behavior induced by coccinellids and other predators may also play a role in aphid dispersal. Roitberg et al. (1979) demonstrated that, unless the plant is in decline, *A. pisum* rarely moved between plants. However, if there was a predator present, the aphids changed plants frequently. Because of this they hypothesized that predator presence may have an important role in mediating aphid dispersal. If this is the case, the higher dropping rates found in our *C. septempuncatata* treatment could serve to facilitate the dispersal of aphids (Roitberg et al., 1979) and by extension, the transmission of aphid-vectored plant diseases (Evans, 1991).

In this study we went beyond comparison of the overall functional response in several important aspects to provide additional insight into how the introduction this exotic organism may impact agricultural systems. These include calculation of q-values for each coccinellid species and quantification of both consumptive and non-consumptive effects. The functional response served as an indicator of the potential impact of an exotic species. We found that *C. sepetempunctata* had higher predatory efficiency and a stronger consumptive impact on *A. pisum* populations than *C. novemnotata,* suggesting that it may be more effective at controlling aphid populations. This data was further supported by the lower q-value calculated for *C. septempunctata*. A decline in the density of pea aphids in Utah associated with the invasion of *C. septempunctata* supports this prediction (Evans, 2004).

However, we also found that *C. septempunctata* is so effective that it has the potential to cause aphid populations to crash, indicating that it may have a less stable relationship with *A. pisum* than *C. novemnotata* does. Although our separate experiments do not allow us to quantitatively combine predation and dropping rates, the greater impact on aphid populations and the associated greater instability estimated for *C. septempunctata* would theoretically be exacerbated by the higher rates of dropping caused by this exotic predator. Clearly, many other factors such as the ability to locate patches of prey, the ability to locate viable overwintering sites, and the ability to disperse over large distances to find these resources will play a large role, but based on our data we predict that a complex of coccinellids that contains *C. septempunctata* instead of *C. novemnotata* will have a greater ability to suppress pea aphid populations but could potentially be less stable.

Acknowledgment

References

Barratt, B., Ferguson, C., Goldson, S., Phillips, C., Hannah, D., 2000. Predicting the risk from biological control agent introductions: A New Zealand Approach. In: Nontarget Effects of Biological Control. Kluwer Academic Publishers, pp. 60–75.

Beddington, J.R., Free, C.A., Laston, J.H., 1978. Characteristics of successful natural enemies in models of biological control of insect pests. Nature 273, 513–519.

Bollache, L., Dick, J.T.A., Farnsworth, K.D., Montgomery, W.I., 2008. Comparison of the functional responses of invasive and native amphipods. Biol. Lett. 4, 166–169.

Bolker, B.M., 2008. Ecological Models and Data in R. Princeton University Press.

Brodsky, L.M., Barlow, C.A., 1986. Escape responses of the pea aphid, *Acyrthosiphon pisum* Harris (Homoptera: Aphididae): influence of predator type and temperature. Can. J. Zool. 64, 937–939.

Debach, P., Rosen, D., 1991. Biological Control: Definition and Scope. Cambridge University Press.

Didham, R., Tylianakis, J., Hutchison, M., Ewers, R., Gemmell, N., 2005. Are invasive species the drivers of ecological change? Trends Ecol. Evol. 20, 471–474.

Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H., Lewis, S., Leung, S., Minchin, D., Caffrey, J., Alexander, M., Maguire, C., et al., 2013. Ecological impacts of an invasive predator explained and predicted by comparative functional responses. Biol. Invasions 15, 837–846.

Dixon, A.F.G., 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). Trans. R. Entomol. Soc. Lond. 110, 319–334.

Driesche, R., Bellows, T.J., 1996. Biological Control. Chapman & Hall.

ElHag, E.T., Zaitoon, A., 1996. Biological parameters for four coccinellid species in central Saudi Arabia. Biol. Control 7, 316–319.

Elliot, N., Kieckhefer, R., Kauffman, W., 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecol 105, 537–544.

Evans, E.W., 1991. Intra versus interspecific interactions of lady beetles (Coleoptera: Coccinellidae) attacking aphids. Oecol 87, 401–408.

Evans, E.W., 2004. Habitat displacement of North American ladybirds by an introduced species. Ecology 85, 637–647.

Evans, H.F., 1976. The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrthosiphon pisum*. Ecol. Entomol. 1, 85–90.

Fill, A., Long, E.Y., Finke, D.L., 2012. Non-consumptive effects of a natural enemy on a non-prey herbivore population. Ecol. Entomol. 37, 43–50.

Finlayson, C., Alyokhin, A., Gross, S., Porter, E., 2010. Differential consumption of four aphid species by four lady beetle species. J. Insect Sci. 10, 1–10.

Fothergill, K., Tindall, K.V., 2010. Lady beetle (Coleoptera: Coccinellinae) occurrences in Southeastern Missouri agricultural systems: differences between 1966 and present. Coleopts Bull. 64, 379–382.

Gardiner, M.M., O'Neal, M.E., Landis, D.A., 2011. Intraguild predation and native lady beetle decline. PLoS One 6, e23576.

Gordon, R.D., 1985. The Coccinellidae (Coleoptera) of America North of Mexico. J. New York Entomol. Soc. 93, 1–912.

Greathead, D.J., Greathead, A.H., 1992. Biological control of insect pests by insect parasitoids and predators: the BIOCAT database. Biocon News Info. 13, 61N–68N.

Harmon, J.P., Stephens, E., Losey, J., 2007. The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. J. Insect Conserv., 85–94.

Hodek, I., Honek, A., 1996. Ecology of Coccinellidae. Kluwer Academic Publishers.

Kestrup, A.M., Dick, J., Ricciardi, A., 2011. Interactions between invasive and native crustaceans: differential functional responses of intraguild predators towards juvenile hetero-specifics. Biol. Invasions 13, 731–737.

JMP pro, Version 10. SAS Institute Inc., Cary, NC, 1989–2013.

Legrand, A., Barbosa, P., 2000. Pea Aphid (Homoptera: Aphididae) fecundity, rate of increase, and within-plant distribution unaffected by plant morphology. Environ. Entomol. 29, 987–993.

Lester, P.J., Harmsen, R., 2002. Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. J. Appl. Ecol. 39, 455–468.

Losey, J.E., Denno, R.F., 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79, 2143–2152.

Losey, J., Perlman, J., Kopco, J., Ramsey, S., Hesler, L., Evans, E., Allee, L., Smyth, R., 2012. Potential causes and consequences of decreased body size in field populations of *Coccinella novemnotata*. Biol. Control 61, 98–103.

Montgomery, M.E., Nault, L.R., 1977. Comparative response of aphids to the alarm pheromone,(E)-ß-farnesene. Entomol. Exp. Appl. 22, 236–242.

Obrycki, J.J., Elliot, N.C., Giles, K.L., 2000. Coccinellid introductions: potential for and evaluation of nontarget effects. In: Follet, P.A., Duan, J.J. (Eds.), Nontarget Effects of Biological Control. Kluwer Academic Publishers.

Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86, 501–509.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available from: <http://www.R-project.org/>.

Raak-van den Berg, L., 2012. Intraguild Predation Behavior of Ladybirds in Semi-Field Experiments Explain Invasion Success of Harmonia axyridis. PLos ONE 7, e40681.

Rodriguez-Saona, C., Miller, J., 1995. Life history traits of *Hippodamia convergens* (Coleoptera: Coccinellidae) after selection for fast development. Biol. Control 5, 389–396.

Roger, C., Coderre, D., Vigneault, C., Boivin, G., 2001. Prey discrimination by a generalist coccinellid predator: effect of prey age or parasitism? Ecol. Entomol. 26, 163–172.

Roitberg, B., Myers, J., 1977. Adaptation of alarm pheromone responses of the pea aphid *Acyrthosiphon pisum* (Harris). Can. J. Zool. 56, 103–108.

Roitberg, B., Myers, J., 1997. Behavioural and physiological adaptations of pea aphids (Homoptera: Aphididae) to high ground temperatures and predator disturbance. Can. Entomol. 111, 515–519.

Roitberg, B., Myers, J., Frazer, B.D., 1979. The influence of predators on the movement of apterous pea aphids between plants. J. Anim. Ecol. 48, 111–122.

Ruth, W.E., McNew, R.W., Caves, D.W., Eikenbary, R.D., 1975. Greenbugs (Homoptera: Aphididae) forced from host plants by Lysiphles testaceipes (Hymenoptera: Braconidae). Entomophaga 20, 65–72.

Schaefer, P.W., Dysart, R.J., Specht, H.B., 1987. North American distribution of Coccinella septempunctata (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. Environ. Entomol. 16, 368–373.

Sengonca, C., Frings, B., 1985. Interference and competitive behavior of the aphid predators, Chrysoperla carnea and Coccinella septempunctata in the laboratory. Entomophaga 30, 245–251.

Sharov, A., n.d. Quantitative population ecology. Predator–prey model with functional and numerical responses. <http://home.comcast.net/~sharov/PopEcol/lec10/fullmod.html>. (accessed June 2013).

Stiling, P., Simberloff, D., 2000. The frequency and strength of nontarget effects of invertebrate biological control agents of plant pests and weeds. In: Follet, P., Duan, J.J. (Eds.), Nontarget Effects of Biological Control. Kluwer Academic Publishers, pp. 32–43.

Wheeler Jr, A., Hoebeke, E., 1995. Coccinella novemnotata in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proc. Entomol. Soc. Wash., 103–111.

Wyatt, I.J., White, P.F., 1977. Simple estimation of intrinsic increase rates for aphids and tetranychid mites. J. Appl. Ecol. 14, 757–766.