



Changes in a lady beetle community following the establishment of three alien species

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Abstract

A number of recent studies indicated that establishment of exotic lady beetles (Coleoptera: Coccinellidae) may have adverse effects on native lady beetle species. In the present study, we analyzed changes in coccinellid community inhabiting potato crops in northern Maine over the past 31 years. Prior to 1980, lady beetle communities were comprised almost exclusively of the two native species, *Coccinella transversoguttata* Brown and *Hippodamia tredecimpunctata* (Say). Starting 1980, an exotic species *Coccinella septempunctata* L. became permanently established in potato crops and quickly started to dominate lady beetle community. Two other exotic species, *Harmonia axyridis* (Pallas) and *Propylea quatordecimpunctata* (L.) became prominent members of the lady beetle community in 1995 and 1996. Invasion by exotic species was followed by a significant decline in the abundance of *C. transversoguttata* and *H. tredecimpunctata*, and a significant increase in the overall diversity of lady beetle community. The abundance of aphid prey was substantially reduced after the establishment of *H. axyridis*. The observed trends demonstrate the profound effects that exotic natural enemies may have on target and non-target native species, and highlight the importance of their thorough evaluation before initiating biological control programs.

Introduction

Invasion by exotic species has become one of the major environmental problems in a variety of ecosystems all over the world. Expanding human transport and commerce have led to a dramatic increase in the geographic scope, frequency, and number of exotic introductions (Mack et al. 2000). Furthermore, numerous species have been deliberately introduced into new locations for biological control of economically important pests (De Bach and Rosen 1991). Historically, most scientists and the general public viewed biological control as an efficient, low-cost, and environmentally safe approach to pest management

(De Bach and Rosen 1991). However, serious concerns over negative impacts of natural enemy introductions have been recently raised by a number of prominent ecologists and conservation biologists (see reviews in Howarth 1991; Lockwood 1993, 1996; Simberloff and Stiling 1996; Hopper 1998). Therefore, a better understanding of natural enemy fate following introduction and its impacts on the new environment is essential for advancing theory and practice of biological control.

Lady beetles (Coccinellidae) are one of the most important groups that prey on pest insects, particularly on aphids and other Homoptera. Spectacular success of the introduced *Vedalia*

beetle, *Rodolia cardinalis* (Mulsant) in controlling cottony cushion scale in California in late 19th century has ever since been a textbook example illustrating accomplishments of biological control (De Bach and Rosen 1991). Overall, a total of 179 lady beetle species have been deliberately or inadvertently introduced into the USA. Of those, 26 species became established, often contributing to the suppression of insect pests (Gordon 1985). Unfortunately, a number of recent studies indicated that establishment of exotic lady beetles may have adverse effects on native lady beetle species. Increased competition for food, intra-guild predation, and the combination of those two factors were suggested as possible explanations to the observed negative interactions among the species (Evans 1991, 2000; Hironori and Katsuhiko 1991; Elliott et al. 1996; Obrycki et al. 1998; Kajita et al. 2000).

Coccinella septempunctata L., *Harmonia axyridis* (Pallas), and *Propylea quatordecimpunctata* (L.) are three species of exotic lady beetles that are currently very common in eastern North America (Day et al. 1994; Wheeler and Hoebeke 1995; Hoebeke and Wheeler 1996; Ellis et al. 1999). All three of them are Old World in origin. *C. septempunctata* and *P. quatordecimpunctata* are widespread paleoartic species (Gordon 1985; Hoebeke and Wheeler 1996), while *H. axyridis* occurs in southern Siberia, Manchuria, China, Taiwan, Korea, Japan, Ryukyu Islands, and Bonin Islands (Gordon 1985; Chapin and Brou 1991). The exact mode of their introduction to North America is unknown. At one time or another, all three species have been deliberately released for biological control of pest aphids (Shands et al. 1972; Gordon 1985; Schaefer et al. 1987; Day et al. 1994). However, subsequent surveys at or near release sites usually failed to detect the establishment of these species. On the opposite, most of them were first recovered in the vicinity of seaports (Day et al. 1994). Therefore, it is generally assumed that their current populations in North America resulted from inadvertent introductions with ship cargoes (Day et al. 1994; Wheeler and Hoebeke 1995).

Based on an extensive literature review, Wheeler and Hoebeke (1995) suggested that invasion by *C. septempunctata*, a polyphagous lady beetle of paleoartic origin, might have been

responsible for the observed dramatic decline of the native lady beetle *Coccinella novemnotata* Herbst. Similarly, Elliott et al. (1996) observed 20–32-fold decrease in the abundance of native *C. transversoguttata* Brown and *Adalia bipunctata* (L.) after *C. septempunctata* establishment in alfalfa, corn, and small grain fields in eastern South Dakota. In turn, *C. septempunctata* has been recently replaced by *H. axyridis* (Pallas), in West Virginia apple orchards (Brown and Miller 1998). Clearly, invasion by exotic species is causing profound modifications in lady beetle communities, and a better understanding of such changes has important theoretical and practical implications.

Lady beetle populations commonly exhibit high temporal variability (Kieckhefer and Elliott 1990; Evans and Youssef 1992). Therefore, long-term studies conducted at the same location are essential to reliably delineate trends and patterns in ecological processes taking place in their populations (Elliott et al. 1996). Elliott et al. (1996) and Brown and Miller (1998) obtained extremely valuable information on the impacts of exotic lady beetles using 13- and 16-year data sets collected in South Dakota and West Virginia, respectively. In the present study, we further expanded this line of research by analyzing changes in coccinellid community inhabiting potato crops in northern Maine over the past 31 years.

Materials and methods

Data used in the present study have been collected from the untreated control plots set-up as a part of insecticide trials at the Aroostook Research Farm, Presque Isle, Maine. The trials were conducted every year between 1971 and 2001, except for 1976 and 1979. Experimental protocols were very similar each year of investigations. Approximately 17.7 m long and four row wide experimental plots were planted to certified seed potato tubers that were cut into 75–80 g pieces prior to planting. The distance between the rows was ca. 90 cm, and seed spacing was ca. 35 cm. Approximately 1.8 m was left between the plots within each block, and blocks were spaced at ca. 3 m. All plots were fertilized with NPK fertilizer

at planting and sprayed weekly with fungicides to control fungal diseases of potatoes. Between 5 and 30 plots were planted each year, depending on the number of chemicals tested. Potatoes were grown in a two-year rotation with small grains.

Twenty-five plants were randomly selected at weekly intervals from the middle two rows of each plot and visually examined for the presence of lady beetles. The number of adult *Hippodamia tredecimpunctata* (Say), *Coccinella transversoguttata* Brown (two native species), as well as the number of exotic *C. septempunctata* L., *H. axyridis* (Pallas), and *P. quatordecimpunctata* (L.) present on each selected plant was recorded. Together, these five species usually accounted for 100% of all lady beetles present at the potato plots. Lady beetles belonging to other species were found sporadically during only 3 years of the 31-year study. Those were recorded as 'other' without attempting to identify them to a species. Additionally, the number of potato-colonizing aphids [potato aphid, *Macrosiphum euphorbiae* (Thomas), buckthorn aphid, *Aphis nasturtii* Kaltentbach, and green peach aphid, *Myzus persicae* (Sulzer)] infesting one top, one middle, and one bottom leaf of each selected plant were counted at weekly intervals throughout the growing season. For operational reasons, the number of plants sampled at each plot was reduced to 20 starting 1995.

For each year of the study, mean seasonal insect density was calculated separately for each replication. Densities were expressed on per plant (for lady beetles) or per leaf (for aphids) basis. Because there is no evidence that any aphid species is a preferred prey for ladybeetles, all three of them were pooled together. The seasonal mean values were used for further statistical analysis.

Relative abundance of different lady beetle species at different years of the study was compared using chi-square test (PROC FREQ; SAS Institute 1999). Species diversity was characterized using the Berger–Parker species dominance index (d) and the Shannon diversity index (H') (Magurran 1988). Differences in species diversity among years, as well as differences in total abundances of lady beetles and their aphid prey were analyzed by ANOVA (PROC GLM; SAS Institute 1999) (Magurran 1988; Wright and DeVries 2000). Data normality was checked before the

analyses using the Wilk–Shapiro test ($P = 0.01$) (PROC UNIVARIATE; SAS Institute 1999). Because of its non-normal distribution, the data were then transformed using rank transformations (Conover and Iman 1981) or arcsine transformations (Zar 1999). Mean and standard errors presented in this article were calculated from the non-transformed data only. ANOVA was followed by orthogonal multiple contrasts that were designed *a priori* (Zar 1999) to test the differences between various time periods. Those were: (1) time period before 1980 when lady beetle complex consisted almost exclusively of native beetles vs time period starting 1980 when exotic beetles became well-established within experimental plots; (2) time period between 1980 and 1995 when *C. septempunctata* was the major exotic species vs time period starting 1995 when *H. axyridis* and *P. quatordecimpunctata* also became prominent part of the community. Mutual interactions of different lady beetle species was analyzed using Spearman's rank correlations (PROC CORR; SAS Institute 1999), and the impact of those species on the abundance of aphid prey was analyzed by multiple regression (PROC REG; SAS Institute 1999).

Additional information on lady beetle populations in the untreated control plots for the period between 1955 and 1964 was obtained from the archive maintained at the Aroostook Experiment Farm. Unfortunately, those records contained only information on relative abundance of different species, and not on their population densities. Also, no data were available for the period between 1964 and 1971. Therefore, only data collected starting 1971 were included in the statistical analysis.

Results

The relative abundance of different lady beetle species varied substantially among the years (Figures 1 and 2), with the observed difference being highly significant ($\chi^2 = 452.8$, $df = 28$, $P < 0.0001$). Prior to 1980, lady beetle communities were comprised almost exclusively of the two native species, *H. tredecimpunctata* and *C. transversoguttata*. Despite extensive releases of laboratory-reared eggs and larvae conducted in

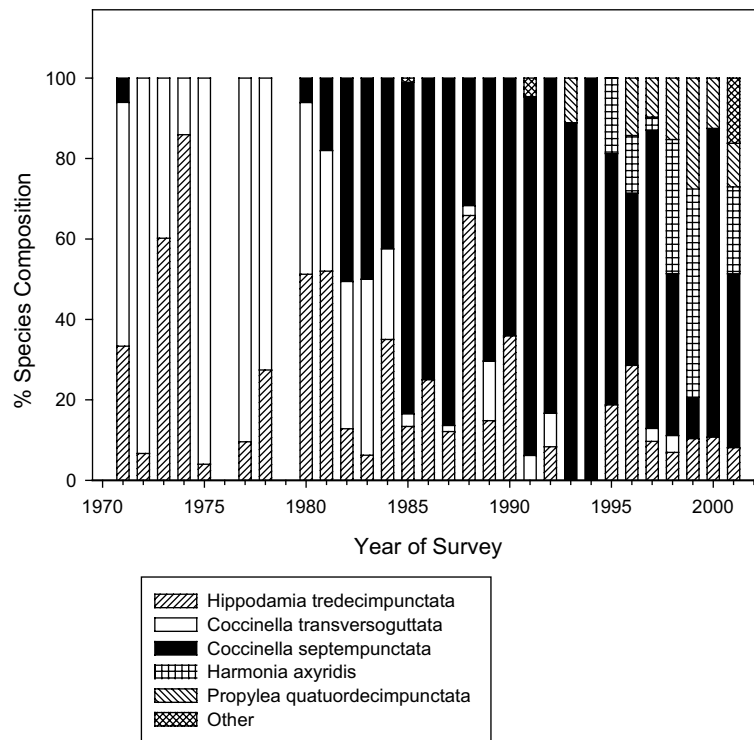


Figure 1. Relative abundance of different lady beetle species in untreated potato plots in northern Maine in 1971–2001.

1964–1969 (Shands et al. 1972), *C. septempunctata* was virtually absent from experimental plots until 1980. Starting 1980, however, this species has become permanently established, and its relative abundance skyrocketed from 6.1% in 1980 to 100% in 1994 (Figure 1). Concomitantly, the relative abundance of *H. tredecimpunctata* and *C. transversoguttata* decreased dramatically, with no *C. transversoguttata* encountered for periods up to several years. *P. quatuordecimpunctata* was first observed in 1993, and *H. axyridis* was first observed in 1995. In the following years, both species became prominent members of the lady beetle community.

There were highly significant negative correlations between the abundance of native *C. transversoguttata* and all three species of exotic lady beetles (Table 1). Abundance of *H. tredecimpunctata* was negatively correlated with the abundance of *C. septempunctata*, but not the other two exotic species (possibly because *H. tredecimpunctata* populations had already been decimated at the time of their establishment in potato plots). In the same time, abundances of exotic

species in most cases were positively correlated with each other (Table 1).

There were significant fluctuations in the diversity of lady beetle communities as evidenced both by the Berger–Parker species dominance index ($F = 5.13$, $df = 28, 292$, $P < 0.0001$) and the Shannon diversity index ($F = 6.25$, $df = 28, 292$, $P < 0.0001$). Species diversity, on average, increased following the establishment of the first exotic lady beetle, *C. septempunctata*, in 1980. Subsequent establishment of *H. axyridis* and *P. quatuordecimpunctata* led to further elevation in species diversity (Table 2).

Absolute abundance of lady beetles (all species pooled together) varied significantly among the years ($F = 10.84$, $df = 28, 292$, $P < 0.0001$). Fewer beetles were encountered at the experimental plots after 1980 (Table 2). However, this difference was largely due to unusually high beetle populations in 1978 (Figure 3). When that year was dropped from the analysis, the difference between those two time periods became statistically insignificant ($F = 0.49$, $P = 0.4863$). In the same time, more beetles were observed between

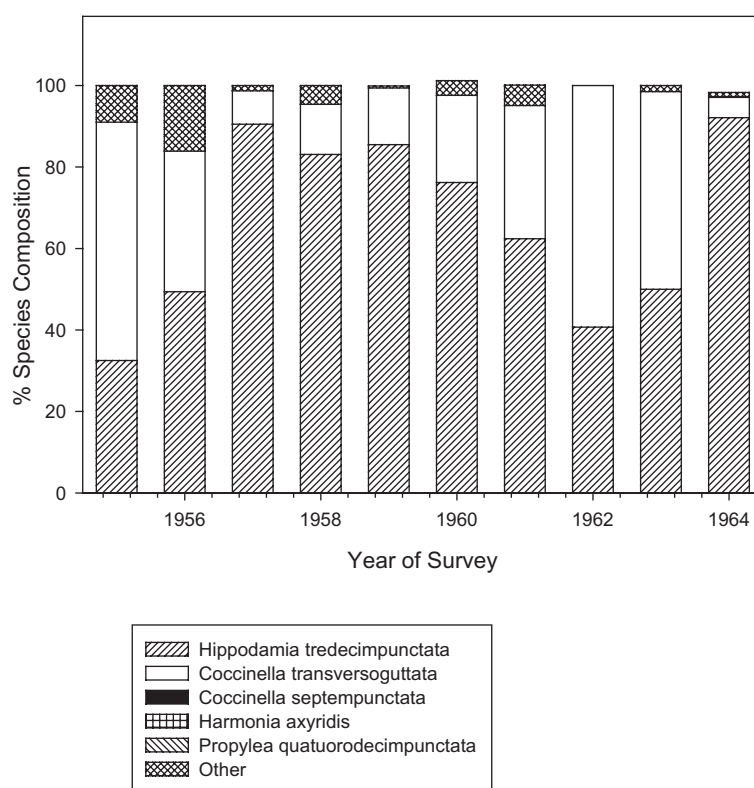


Figure 2. Relative abundance of different lady beetle species in untreated potato plots in northern Maine in 1955–1964.

Table 1. Spearman's rank correlation among densities of lady beetle populations in untreated potato plots in northern Maine.

	<i>C. transversoguttata</i>	<i>C. septempunctata</i>	<i>H. axyridis</i>	<i>P. quatordecimpunctata</i>	Other species
<i>H. tredecimpunctata</i>					
R_s	0.2574	-0.1241	-0.0840	-0.0149	-0.0760
P -value	<0.0001	0.0180	0.1100	0.7778	0.1483
<i>C. transversoguttata</i>					
R_s		-0.2291	-0.1763	-0.1330	-0.0650
P -value		<0.0001	0.0007	0.0112	0.2165
<i>C. septempunctata</i>					
R_s			0.0849	0.1740	0.0437
P -value			0.1063	0.0009	0.4061
<i>H. axyridis</i>					
R_s				0.4142	0.1425
P -value				<0.0001	0.0065
<i>P. quatordecimpunctata</i>					
R_s					0.0763
P -value					0.1470

1980 and 1995 than between 1995 and 2001 (Table 2). Establishment of *C. septempunctata* led to a pronounced reduction in density of *H. tredecimpunctata* and *C. transversoguttata* populations, while establishment of *H. axyridis* and

P. quatordecimpunctata had a statistically significant impact only on *C. transversoguttata* (Table 2).

Mean number of aphids infesting sampled leaves varied significantly among the years of the study ($F = 21.914$, $df = 28, 292$, $P < 0.0001$).

Table 2. Effect of *C. septempunctata*, *H. axyridis*, and *P. quatordecimpunctata* establishment on lady beetle community in untreated potato plots in northern Maine.

	<i>C. septempunctata</i>				<i>H. axyridis</i> and <i>P. quatordecimpunctata</i>			
	Before	After	F^c -value	P -value	Before	After	F^c -value	P -value
Mean species diversity								
Berger index	0.8733	0.7771	4.73	0.0305	0.7430	0.6743	14.27	0.0002
(SE)	0.0152	0.0135			0.0221	0.0285		
Shannon index	0.2530	0.4372	8.02	0.0049	0.5004	0.6621	19.83	<0.0001
(SE)	0.0268	0.0257			0.0415	0.0617		
Mean lady beetle density ^a								
All species	0.0265	0.0212	8.26	0.0043	0.0230	0.0276	16.53	<0.0001
(SE)	0.0026	0.0013			0.0024	0.0030		
<i>H. tredecimpunctata</i>	0.0120	0.0039	24.82	<0.0001	0.0057	0.0028	0.46	0.4995
(SE)	0.0016	0.0004			0.0008	0.0006		
<i>C. transversoguttata</i>	0.0144	0.0034	206.01	<0.0001	0.0083	0.0004	8.85	0.0031
(SE)	0.0018	0.0005			0.0011	0.0002		
Mean aphid density ^b	5.4828	2.7039	21.18	<0.0001	3.4154	0.6155	158.3	<0.0001
(SE)	0.3177	0.1173			0.1722	0.0729		

^a Per sampled plant (see text for sampling details).

^b Per sampled leaf (see text for sampling details).

^c Single degree of freedom orthogonal contrasts (Zar 1999).

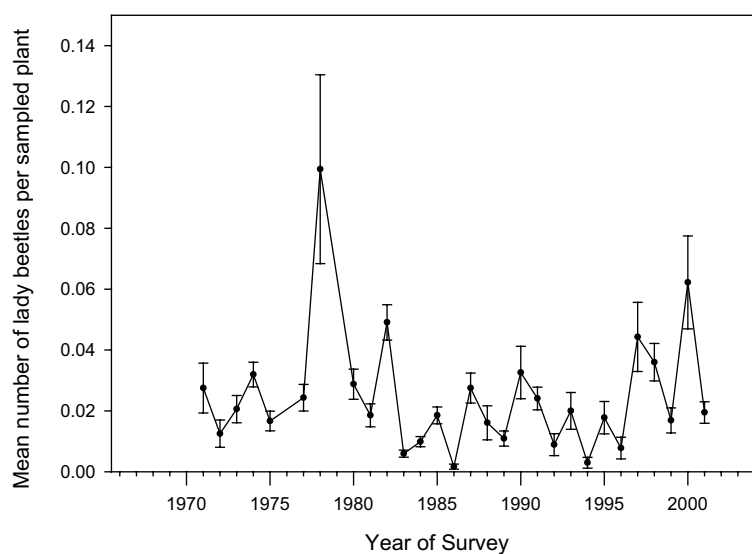


Figure 3. Population density of lady beetles (all species combined) in untreated potato plots in northern Maine in 1971–2001.

Noticeably fewer aphids were encountered at the experimental plots after establishment of exotic lady beetles, especially *H. axyridis* and *P. quatordecimpunctata* (Figure 4; Table 2). Multiple regression analysis indicated that lady beetle density had a highly significant impact on aphid density ($F = 9.0$, $df = 6, 356$, $P < 0.0001$), although

the majority of observed variation was better explained by other factors ($R^2 = 0.13$). Among all species, only densities of *H. tredecimpunctata* and *H. axyridis* were predictive of aphid density (Table 3). As evidenced by regression coefficients (Table 3), high densities of *H. tredecimpunctata* observed at experimental plots predicted that

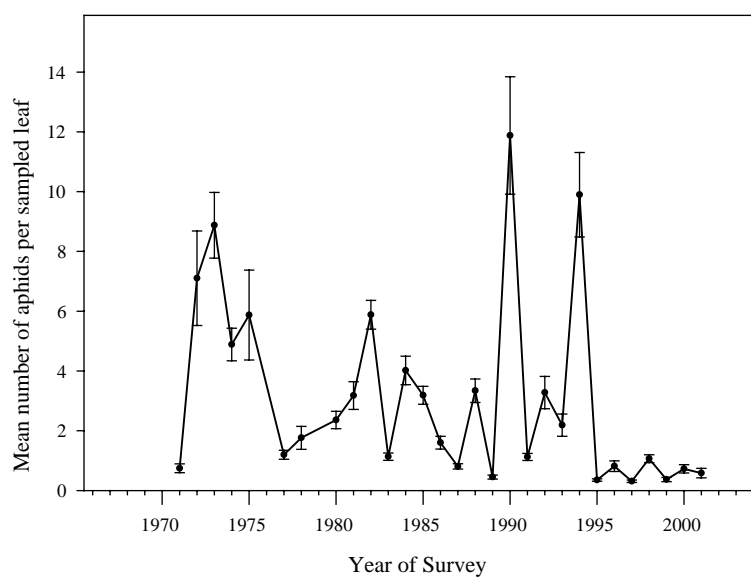


Figure 4. Population density of potato-colonizing aphids in untreated potato plots in northern Maine in 1971–2001.

Table 3. Multiple regression results testing for effects of different lady beetle species on resident aphid populations in untreated potato plots in northern Maine.

Variable	<i>b</i>	SE	<i>t</i>	<i>P</i> -value
Intercept	176.86	7.58	23.34	<0.0001
<i>H. tredecimpunctata</i>	1783.69	451.33	3.95	<0.0001
<i>C. transversoguttata</i>	410.64	386.94	1.06	0.2893
<i>C. septempunctata</i>	- 227.13	450.22	-0.50	0.6142
<i>H. axyridis</i>	-6658.82	1791.26	-3.72	0.0002
<i>P. quatordecimpunctata</i>	-3710.91	2200.18	-1.69	0.0925
Other species	-5041.58	4146.73	-1.22	0.2249

aphid densities would also be high, while high densities of *H. axyridis* predicted that aphid densities would be low.

Discussion

Both density of lady beetle populations and relative abundance of different species comprising the lady beetle community varied significantly between the years of our study. Such a variation is quite common for this group of insects (Kieckhefer and Elliott 1990; Evans and Youssef 1992), and often makes it difficult to detect changes in their communities (Evans 2000). However, shifts in the species composition observed in our study appear to be consistent over long periods of time

(Figures 1 and 2). At first, the community previously consisting of native species became dominated by *C. septempunctata*. This is very similar to the situation observed by Wheeler and Hoebeke (1995) at a number of locations at northeastern North America, and by Elliott et al. (1996) in South Dakota. More recently, *C. septempunctata* domination was challenged by the other two exotic species, *H. axyridis*, and *P. quatordecimpunctata*. Brown and Miller (1998) reported comparable trend in West Virginia apple orchards. Therefore, it appears that changes observed in our study agree with broader changes occurring in lady beetle communities at a large geographic scale.

Interestingly, there was a highly significant positive correlation between the densities of

H. axyridis and *P. quatordecimpunctata*, as well as between the densities of *P. quatordecimpunctata* and *C. septempunctata*. This implies the possibility of biotic facilitation, a phenomenon when two or more invading species enhance each other's survival and/or population size (Simberloff and Von Holle 1999). Biotic facilitation is probably more common in nature than previously thought (Simberloff and Von Holle 1999). However, our data are far from sufficient for making definite conclusions on this subject. It seems counter-intuitive that competitors would engage in facilitative interactions, and it is possible that the observed correlation is caused by some external factor having a similar impact on populations of different invading species.

Replacement of native lady beetles by *C. septempunctata* did not appear to cause significant reduction in the number of potato-colonizing aphids (Figure 4), just as it was the case in the study by Evans (1991). In the same time, establishment of *H. axyridis* and *P. quatordecimpunctata* coincided with a dramatic decrease in the abundance of their prey (Figure 4). Multiple regression analysis indicated that *H. axyridis* density had a significant influence on the density of aphid populations. No such effect was detected for *P. quatordecimpunctata*. Brown and Miller (1998) observed a similar suppression of pest aphids after *H. axyridis* had become a dominant species at their study sites, suggesting that *H. axyridis* is probably a superior biological control agent of aphid pests when compared with *C. septempunctata*.

Classical biological control via introduction of exotic natural enemies has come under increasing scrutiny because of its possible detrimental effects on non-target species (Howarth 1991; Lockwood 1993, 1996; Simberloff and Stiling 1996; Hopper 1998). Among other things, such negative interactions are caused by predation and competition for common resources, as was probably the case with the lady beetles observed in the present study. Although invasion of *C. septempunctata*, *H. axyridis* and *P. quatordecimpunctata* is commonly thought to originate from inadvertent introductions rather than from deliberate releases (Day et al. 1994; Wheeler and Hoebeke 1995), our results still demonstrate the profound effects that exotic natural enemies may have on non-tar-

get native species. However, it is yet unknown if those effects have negative environmental consequences from the conservation standpoint.

Despite dramatic reduction in their relative abundances, both *C. transversoguttata* and *H. tredecimpunctata* persisted at low densities in potato plots after the establishment of exotic species (Figure 1). As a result, the invasion increased the species diversity at the experimental plots (Table 3). Furthermore, potato is as exotic a species in northern Maine as *C. septempunctata*, *H. axyridis*, or *P. quatordecimpunctata*. In spite of usually being able to utilize a variety of different habitats, at least some aphidophagous lady beetle species have been shown to display preference toward certain environments (Honek 1985). Therefore, it has been argued that arrival of the invaders might simply cause 'habitat compression' for native lady beetles (Evans 2000). This entails retreat to ancestral habitats, where native species may have competitive advantage over the newcomers. Also, our study has been conducted using a small sampling unit at a single geographical location, and untreated plots were embedded within insecticide trial plots. All this does not allow us to make far-reaching conclusions solely based on our data. Further investigations on a larger spatial scale are required to fully assess the environmental impacts of exotic lady beetles. Knowing these impacts will improve our ability to evaluate the safety of entomophagous agents considered for introduction in biological control programs.

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References

- Brown MW and Miller SS (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News* 109: 136-142
- Chapin JB and Brou VA (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United

- States (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 93: 630–635
- Conover WJ and Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* 35: 124–129
- Day WH, Prokrym DR, Ellis DR and Chianese RJ (1994) The known distribution of the predator *Propylea quatordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in eastern North America. *Entomological News* 105: 244–256
- De Bach P and Rosen D (1991) *Biological Control by Natural Enemies*. Cambridge University Press, Cambridge, 440 pp
- Elliott N, Kieckhefer R and Kauffman W (1996) Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* 105: 537–544
- Ellis DR, Prokrym DR and Adams RG (1999) Exotic lady beetle survey in northeastern United States: *Hippodamia variegata* and *Propylea quatordecimpunctata* (Coleoptera: Coccinellidae). *Entomological News* 110: 73–84
- Evans EW (1991) Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. *Oecologia* 87: 401–408
- Evans EW (2000) Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in western North America. *European Journal of Entomology* 97: 469–474
- Evans EW and Youseff NN (1992) Numerical responses of aphid predators to varying prey density among Utah alfalfa fields. *Journal of Kansas Entomological Society* 65: 30–38
- Gordon RD (1985) The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* 93: 1–912
- Hironori Y and Katsuhiko S (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 153–163
- Hoebeker ER and Wheeler AG (1996) Adventive lady beetles (Coleoptera: Coccinellidae) in the Canadian Maritime provinces, with new eastern US records of *Harmonia quadripunctata*. *Entomological News* 107: 281–290
- Honek A (1985) Habitat preferences of aphidophagous coccinellids (Coleoptera). *Entomophaga* 30: 253–264
- Hopper KR (1998) Assessing and improving the safety of introductions for biological control. *Phytoprotection* 79(S): 84–93
- Howarth FG (1991) Environmental impacts of classical biological control. *Annual Review of Entomology* 36: 485–509
- Kajita Y, Takano F, Yasuda H and Agarwala BK (2000) Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Applied Entomology and Zoology* 35: 473–479
- Kieckhefer RW and Elliott NC (1990) A 13-year survey of the aphidophagous Coccinellidae in maize fields in eastern South Dakota. *Canadian Entomologist* 122: 579–581
- Lockwood JA (1993) Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environmental Entomology* 22: 503–518
- Lockwood JA (1996) The ethics of biological control: understanding the moral implications of our most powerful ecological technology. *Agriculture and Human Values* 13: 2–19
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M and Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710
- Magurran AE (1988) *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, New Jersey, 179 pp
- Obyrcki JJ, Giles KL and Ormond AM (1998) Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environmental Entomology* 27: 1280–1288
- SAS Institute, Inc. (1999) SAS OnLine Doc, Version 8. Cary, North Carolina
- Schaefer PW, Dysart RJ and Specht HB (1987) North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. *Environmental Entomology* 16: 368–373
- Shands WA, Simpson GW, Wave HE and Gordon CC (1972) Importance of arthropod predators in controlling aphids on potatoes in northeastern Maine. University of Maine (Orono) Technical Bulletin 54
- Simberloff D and Stiling P (1996) How risky is biological control? *Ecology* 77: 1965–1974
- Simberloff D and Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32
- Wheeler AG and Hoebeker ER (1995) *Coccinella novemnotata* in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 97: 701–716
- Wright RJ and DeVries TA (2000) Species composition and relative abundance of Coccinellidae (Coleoptera) in south central Nebraska field crops. *Journal of Kansas Entomological Society* 73: 103–111
- Zar JH (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, Upper Saddle River, New Jersey, 663 pp