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The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada

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Abstract Reviewing published coccinellid surveys we found that the number of adventive species has increased steadily over the last century while the average proportion of native individuals has remained fairly constant until 1987 followed by a rapid decrease between 1987 and 2006. Seven long-term studies indicated that the total density of coccinellids increased by an average of 14% following establishment of adventive species, but this increase was not significant and in 4 of 7 cases the total density of coccinellids actually decreased following establishment. Similarly, no significant difference was found in comparisons of diversity across all studies. These results illustrate that even with multiple long-term data sets it is currently difficult to make any general conclusions regarding the impact adventive coccinellids have had on native coccinellid assemblages. However, it is clear that specific systems and species have seen major shifts in recent years. For example, adventives have become the dominant species in a third of the assemblages where they are found. Focusing on two formerly common native species, *Adalia bipunctata* and *Coccinella novemnotata*, we show they have become rare in their former ranges and discuss potential explanations for this phenomenon.

Keywords *Adalia* · *Coccinella* · Adventive species · Ladybirds · Aphids

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The importance of coccinellid diversity and abundance

Coccinellids, known as ladybugs, ladybeetles, or ladybird beetles are one of the most common and easily recognizable invertebrate components of almost every terrestrial ecosystem in the US and Canada (Gordon 1985). Species in this family are so ubiquitous and yet so sensitive to environmental conditions that they have been proposed as indicator species (Iperti 1999).

This species complex also contributes to the regulation of many soft-bodied insects, especially those in the order Homoptera, and is valuable in controlling the egg and larval stages of other insects (reviewed in Hodek and Honěk 1996). The services that these predators provide are so well recognized and respected that pest management practices are often designed to take advantage of their pest suppression potential. For example, in alfalfa the decision to take action to suppress aphid populations is based on both aphid and coccinellid densities (e.g., Knowles 2006). Pesticides are not applied even if aphid densities exceed what would be economically damaging levels if the density of coccinellids is high enough to suppress them.

Given their potential to control pest species, many programs have tried to supplement extant populations or introduce new species. Purchasing and releasing natural enemies to augment biological control is a potentially valuable and continually growing practice with coccinellids being one of the most important groups used (Cranshaw et al. 1996). Vast resources have also been expended to introduce and permanently establish coccinellid species that are not native to the Nearctic region. One of the first successes with classical biological in the US involved importing the vedalia beetle, *Rodalia cardinalis*, from Australia to suppress the cottony cushion scale, *Icerya purchasi*, in California. The entire cost of this project is estimated at $2,000 (Pedigo and Rice 2006), approximately $41,000 in 2005 adjusting for inflation. This figure is probably below the average cost of subsequent introductions given the increased level of pre-release research that is usually done. Taking the adjusted figure as an average cost for the 179 coccinellid introductions into North America (Gordon 1985) the total cost of these efforts exceeds 7 million dollars.

Given their charisma and acknowledged importance, it is not surprising that numerous studies have examined the composition of this complex and a smaller but no less important body of literature has related their density and diversity to ecological function. Two clear emergent properties are that coccinellid species vary widely in the level of suppression they exert on various prey species (reviewed in Hodek and Honěk 1996) and that species vary widely in their response to environmental changes (Iperti 1999; Bazzocchi et al. 2004). Thus, long-term regional shifts in species composition may have important implications for the functioning of this complex and its response to environmental changes. In this paper we draw on published surveys to examine the density and composition of aphidophagous coccinellids in the US and Canada over the past hundred years.

Materials & methods

We reviewed the published literature for surveys of adult aphidophagous coccinellids in natural and managed ecosystems throughout the United States and Canada. Despite the importance of a number of coccidophagous coccinellids for biological control in North America, e.g., *Rodolia cardinalis* (DeBach 1964), we focus here on aphidophagous species due to their ubiquitous nature, their dominance in the literature, and their importance in recent purposeful and accidental invasions. Studies were included if there were at least 20 naturally occurring individuals collected, the proportion of native and adventive species was easily determined from the paper, and >95% of individuals were identified to species. Only a very small number of studies included larval information, so for consistency we only used information on adult coccinellids. We extracted multiple data sets if collections were made in distinct large-scale habitats (e.g., two different crops) or if multi-year studies had distinct sampling periods with considerable differences (e.g., before and after an invasion). We determined the average coccinellid assemblage for all other multiyear surveys by calculating the proportion of each species in the assemblage for each year and then averaging across years. For analyses over time we used the midpoint date (rounded up) for these multiyear surveys. We also determined average assemblages in the same manner when surveys took place across multiple but similar habitats (e.g., multiple fields of the same crop). Note that in a few instances (e.g., Putnam 1964) information was not available to calculate the average assemblage in this way and we were forced to use an average assemblage as determined by the author. These criteria resulted in information on 71 coccinellid assemblages from 36 references (Ewing 1914; Fluke 1925; Dobzhansky 1935; Fenton and Howell 1955; Godarzy and Davis 1956; Smith 1958; Putnam 1964; Day 1965; Gagne and Martin 1968; Smith 1971; Wheeler 1971; Watve and Clower 1976; Angalet et al. 1979; Turnock and Turnock 1979; Lee 1980; Dowell and Cherry 1981; Mareida et al. 1992; Elliott et al. 1996; LaMana and Miller 1996; Colunga-Garcia et al. 1997; Hoffmann et al. 1997; Brown and Miller 1998; Colunga-Garcia and Gage 1998; Boiteau et al. 1999; Cormier et al. 2000; Hesler et al. 2000; Wright and DeVries 2000; Wold et al. 2001; Bosque-Perez et al. 2002; Stephens 2002; Brown 2003; Turnock et al. 2003; Alyokhin and Sewell 2004; Evans 2004; Hesler et al. 2004; Musser et al. 2004). We further calculated measures of species richness, the Berger–Parker Dominance Index, as well as Simpson's D and Shannon's H diversity indices for the 62 data sets in which all collected individuals were identified to species (Magurran 1988). Since both diversity indices gave very similar results, we only report Simpson's D here.

Results and discussion

Establishment and increase of adventive species

It is difficult to discuss the status of native species without also considering the data on adventive species. The evidence for a causal relationship between the establishment of adventive species and the decline of native species is by no means conclusive (as we discuss below). However, they have certainly changed the composition of this complex by their presence alone.

At least 179 coccinellid species have been introduced deliberately or inadvertently and 27 have become established in the US and Canada (Fig. 1) (Gordon 1985; Gordon and Vandenberg 1991). It appears that although the establishment of many species has been confirmed, very few have grown to levels where they are commonly found in published surveys.

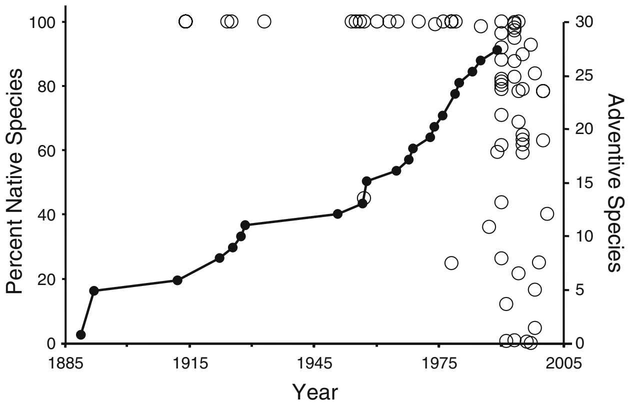

Fig. 1 The cumulative number of adventive species established in the United States and Canada (line) and the percent native species found in surveys of coccinellid assemblages (circles) over time

Only six adventive species were reported in studies of full coccinellid assemblages. Of these, *Coccinella septempunctata* was reported the most often, followed by *Harmonia axyridis*, *Propylea quattuordecimpunctata*, *Coccinella undecimpunctata*, and single occurrences of *Exochomus quadripustulatus* and *Hippodamia variegata*. This is almost certainly due, at least in part, to a sampling bias since most of our data come from surveys in cultivated herbaceous plants (e.g., alfalfa, corn).

Overall, the number of adventive species found within a coccinellid assemblage varied from zero to three with more adventive species being found in more recent studies ($F_{1,61}$=31.5, $P<0.001$), especially those after 1985. At least two of the most common adventive species, *C. undecimpunctata* and *C. septempunctata*, show a pattern of slow increase after establishment followed by a period of rapid growth. More surprising is that for both species this period of rapid growth and rise to prominence was relatively short-lived. *Coccinella undecimpunctata* was the most common species found in potatoes in New York in 1957 (Day 1965) and natural areas in New Jersey in 1978 (Angalet et al. 1979), but was not reported in earlier or later surveys. *Coccinella septempunctata* was the most common species in many surveys in the 1980s but was frequently superseded by another adventive species, *H. axyridis*, in the 1990s. It seems plausible that *H. axyridis*, currently the most common adventive coccinellid in the US and Canada, could undergo a similar decline; however it is unclear which species would replace it since no new species have established in almost 20 years and several key natives have declined to very low densities.

Proportional change in the coccinellid complex

While the number of adventive species has increased over the past 100 years the proportion of native individuals has decreased markedly (Fig. 1). The increase in the number of adventive species has been steady, nearly linear, yet native individuals stayed very close to 100% of the assemblage (with two notable exceptions) until the mid 1980s when assemblages began to vary tremendously in the reported proportion of natives. From 1914 to 1985 native individuals averaged 95.0%±4.0 (1 S.E.) while from 1987 to 2001 natives were significantly lower at 67.5%±4.0 (t_{69}=4.48, P < 0.001). This pattern suggests that if adventive species are the cause of the decline of native species then either the total impact of all these adventive species reached some critical level, or that a subset of the more recently introduced species are causing the bulk of the impact. Based on their extremely high densities and relatively recent introductions, *C. septempunctata* and *H. axyridis* may be responsible for much of the impact to these surveyed native assemblages.

While this proportional decline is striking, care must be taken to not over-interpret these results. A decline in the proportion of natives can result from a decrease in native density or by simply increasing total coccinellid density (natives + adventives) without increasing the density of natives (discussed below). Thus, a complete assessment requires interpreting data on both proportions of native species and their densities.

Numerical change in the coccinellid complex

Most of our collected data sets cannot be used to investigate changes in coccinellid densities. The wide variation in densities across time, space, habitat, and collecting method made it impossible to use most of our data to look for causality by making meaningful comparisons of density across specified time periods (e.g., before and after establishment of an adventive species). Fortunately, we found seven data sets from five studies that measured coccinellid abundances in a single system and with the same method over multiple years that encompassed the establishment of an adventive species (see Table 1). These examples exhibit mixed results in terms of the effect of adventive species on coccinellid densities. Overall the total density of coccinellids increased by an average of 14% (14±21) following establishment. However, the tremendous variation in this study overwhelms any attempt at a single average; in 4 of 7 cases the total density of coccinellids decreased following establishment. This high variability led to no overall difference in total coccinellid density before compared to after invasion (t_5=0.66, P=0.53).

Table 1 Multi-year surveys of coccinellid populations

	Habitat	Units	Total before introduction	Total after introduction	Total after introduction minus focal invader[a]	Adventive Coccinellid
Elliott et al. (1996)	Alfalfa	Ave per 50 sweeps	2.30 1973–1985	3.31 1988–1992	2.69	*Coccinella septempunctata*
	Corn	Ave Per 15-min search	18.4 1973–1985	15.8 1988–1992	14.5	*Coccinella septempunctata*
	Grains	Ave per 50 sweeps	2.90 1973–1985	3.84 1988–1992	3.08	*Coccinella septempunctata*
Colunga-Garcia et al. (1998)	Varied	Ave/210 traps/season	3082.3 1989–1993	2497.5 1994–1998	2112.5	*Harmonia axyridis*
Turnock et al. (2003)	Alfalfa	# Collected (Averaged Per Year)	209.4 1983–1987	459 1988–2001	367.2	*Coccinella septempunctata*
Alyokhin and Sewell (2004)	Potato	Ave per sampled plant	0.0264 1971–1978	0.0212 1980–1995	0.0073	*Coccinella septempunctata*
Evans (2004)	Alfalfa	Ave # per 15 sweeps	4.23 1992–1994	2.34 1998–2001	0.61	*Coccinella septempunctata*

Columns contrast: (1) the total coccinellid populations before and after the arrival and/or establishment of the focal adventive species, and (2) the density of species found before invasion with the density of those same species after invasion

[a] Column is the density of the native coccinellid assemblage with the exception of Colunga-Garcia which includes *C. septempunctata* before and after the introduction of *H. axyridis*

We see a similar trend when looking at only the densities of native coccinellids. In the three studies where total coccinellid density increased, native density also increased following establishment of the adventive species and in the four studies where total density decreased native density decreased as well. Overall the density of native species declined by 16% (16±21) but again there was considerable variation and the difference between before and after establishment was not significant (t_5=0.77, P=0.47).

These studies illustrate that even with multiple long-term data sets it is difficult to make any general conclusions regarding the impact of adventive species establishment on the density of native species or the total density of the coccinellid complex. However, it is clear that in at least some specific cases both the density of native coccinellids and the size of the total coccinellid population was different before compared to after the arrival of an adventive coccinellid (Table 1). However, the direction, magnitude, and significance of such changes varied greatly across studies. Hopefully the discovery of more data will allow us to make firmer conclusions.

Richness, diversity and dominance of native species

In contrast to the low number of adventive species represented in our data set, we found 47 species of native coccinellids with the number of native species found in a single assemblage varying from 0 to 22. The number of native coccinellids found within a given assemblage did not seem to change over time ($F_{1,61}$=0.13, P=0.72), nor was there any relationship between the number of adventive species found in a assemblage and the number of native species ($F_{1,61}$=0.74, P=0.39). Taken together, these results suggest that there is no current evidence for an overall effect of adventive coccinellids on native species richness within a given assemblage.

The diversity of coccinellid assemblages with adventive species was only slightly higher than assemblages with all native species (Simpson's D: 2.67±0.16 at least one adventive species vs. 2.47±0.26 all natives, t_{61}=0.68, P=0.50). However, apart from any biological interactions, we would expect diversity to increase with the addition of adventive species. Therefore in addition to the total diversity of all coccinellids as reported above, we also calculated the diversity of only native coccinellids. In assemblages where adventives were found, the diversity of native coccinellids was of course lower than the total diversity (natives + adventives) of coccinellids in those systems (Simpson's D: 2.28±0.15), but they were still not significantly different from the diversity of assemblages with all native species (t_{60}=0.68, P=0.50). This again suggests that we have no evidence that the presence of adventive species has had a significant negative effect on the diversity of individual native coccinellid assemblages.

Adventive species could influence the composition of coccinellids without having a significant effect on a diversity index by replacing a dominant native species with a dominant adventive species. The coccinellid assemblages of our data set were often dominated by one or a small number of species. For example, on average the single most dominant species accounted for almost 60% of the entire assemblage (Average Berger–Parker's dominance index *d*=0.59). Within assemblages with adventive species, a native was still more likely to be the dominant species (30 vs. 14), but there was no difference in the magnitude of dominance between native dominated and adventive dominated systems (d=0.55±0.03 vs. 0.60±0.04, t_{42}=0.96, P=0.34). Even though native species are more likely to dominate, the shift from almost every assemblage being dominated by native species to almost a third being dominated by adventive species could be very important for the functioning and long-term stability of these assemblages. The dominance of adventive species may expand if adventive species such as *H. axyridis* continue to increase and key native species continue to decline.

A tale of two species: native species in rapid decline

While several authors have suggested that adventive coccinellid species are a major cause for a decline in specific native species (Wheeler and Hoebeke 1995; Ellis et al. 1999; Wise et al. 2001) we cannot support this as a general claim across all coccinellid assemblages. Similarly, Brown (2003) also did not find an impact of *H. axyridis* on the coccinellid complex when looking at original data and a review of studies in apples. Despite the lack of a general decline in natives, it is clear that several formerly common native coccinellid species are now quite rare. In this section we provide some detail on two species, *C. novemnotata* and *A. bipunctata*, that have experienced noted and rapid declines (Obrycki et al. 2000).

Adalia bipunctata

Evidence for decline

A number of coccinellid surveys in agricultural systems have indicated a decline in populations of *A. bipunctata* over the past 10–20 years (Table 2). Some of these most recent surveys indicate *A. bipunctata* is near or below the threshold of detection in places it had regularly inhabited. While these studies on the whole are limited spatially, temporally, and in the types of ecosystems surveyed, they present a consistent picture of decline. Most of these studies have discussed *A. bipunctata* decline in connection with the arrival of an adventive coccinellid. The first prominent report of a decline in *A. bipunctata* found it to be 20 times less abundant after the arrival of *C. septempunctata* (Elliott et al. 1996). Most studies since have shown a negative relationship between *A. bipunctata* populations and *H. axyridis*, but some of these studies have gone further to suggest that *A. bipunctata* abundance may had been declining even prior to *H. axyridis* arrival (Brown and Miller 1998; Colunga-Garcia and Gage 1998; Boiteau et al. 1999).

Potential reasons for decline

The strong temporal correlation between *A. bipunctata*'s decline and the emergence of *C. septempunctata* and *H. axyridis* is suggestive, yet sampling studies cannot demonstrate causality and we have little direct evidence of their interactions in North America. One method of evaluating potential causal factors is to assess their likelihood given studies of coccinellid ecology (e.g., Obrycki et al. 2000). Here, we briefly discuss some factors as they relate specifically to *A. bipunctata*.

The presence of *C. septempunctata* was the dominant explanatory factor for the observation of Elliott et al. (1996) and could explain the observed declines in *A. bipunctata* before *H. axyridis* was observed (Table 2). However, in a review of the ecology of *A. bipunctata* and *C. septempunctata*, Obrycki et al. (2000) concluded that the extent of their interactions should have been limited by spatial and temporal differences in habitat use. Given *A. bipunctata*'s seasonal changes in habitat use (reviewed in Hodek and Honěk 1996), one possible explanation for this apparent discrepancy is a strong source-sink dynamic across the landscape (e.g., Rosenheim 2001). Preferred, wooded habitats may act as source habitats for *A. bipunctata* while the sampled cultivated crops may act as sinks. If so, a habitat generalist such as *C. septempunctata* may generate greater negative effects in areas such as eastern South Dakota where wooded habitats are scarce (Obrycki et al. 2000) than in areas with more of *A. bipunctata*'s preferred habitat.

The ecology of *H. axyridis*, however, suggests that it could have a stronger effect on *A. bipunctata*. *Harmonia axyridis*, like *A. bipunctata* has a broad, polyphagous diet which includes many aphid species, and both use a broad range of habitats while preferring arboreal systems (Hodek and Honěk 1996). Egg and larval cannibalism appears to be important in *H. axyridis* population dynamics (Koch 2003), can be important in coccinellid interactions (Schellhorn 1998), and may be an important part of the interaction between *H. axyridis* and *A. bipunctata*. While *A. bipunctata* seems to have an advantage against *C. septempunctata*

Table 2 Surveys of *A. bipunctata* populations

	Habitat	Sample	Units	Before introduction	After introduction	Adventive Coccinellids
Elliott et al. (1996)	Corn—SD USA	Visual search	# / 15 min search	1973–1985 0.04±0.01	1988–1992 0.002±0.002	*Coccinella septempunctata* (later)
Colunga-Garcia and Gage (1998)	Agricultural landscape—MI USA	Sticky traps	Adults/210 traps/season	1989 115.3 1990 228.4 1991 36.5 1992 31.2 1993 16.6	1994 25.7 1995 10.2 1996 1.2 1997 0.2 1998 1.3	*Coccinella septempunctata, Harmonia axyridis* (later)
Brown and Miller (1998)	Apple trees—WV USA	Visual search	Percent of all ladybirds	1989–1990 9.1% 1991 2.3% 1993 1.7%	1994–1996 0%	*Coccinella septempunctata, Harmonia axyridis* (later)
Boiteau et al. (1999)	Agricultural landscape—NB Canada	Sticky traps (tower)	Total per summer	1992 362 1993 69 1994 51	1995 19	*Coccinella septempunctata, Harmonia axyridis* (later)
Cormier et al. (2000)	Herbs and shrubs—NS Canada	Sweeps	Percent of all ladybirds	1990–1996 >12.5% [a]	1998 0.3%	*Coccinella septempunctata, Hippodamia variegate, Propylea quatuordecimpunctata*
Schellhorn (1998)[b] (earlier), J.P. Harmon *unpubl. data*[b]	Sweet corn—St. Paul, MN USA	Visual search	Adults/plant	1994 0.28 1996 0.44	1999–2000 0 on 960 plants	*Coccinella septempunctata, Harmonia axyridis* (later)
Wold et al. (2001)[b] (earlier), R. L. Koch *pers. comm.* (later)	Sweet corn—Rosemount, MN USA	Visual search	Adults/plant	1998 0.85 1999 0.26	2000–2004 1 on 3978 plants	*Coccinella septempunctata, Harmonia axyridis*

"Before" and "after" columns contrast populations before and after adventive coccinellid(s) arrival. "Adventive coccinellids" are present in both sets of samples unless noted

[a] Within reference is a claim that *A. bipunctata* and another native were 25% of all coccinellids with *A. bipunctata* more common then the other

[b] Samples were averaged across experimental treatments that were each representative of conditions observed in unmanipulated plots

in conspecific egg predation (Hemptinne et al. 2000), that does not seem to be the case against *H. axyridis* (Sato and Dixon 2004) which seems to be well protected against native coccinellids (Cottrell 2004; Sato and Dixon 2004). Moreover, egg cannibalism may be enhanced in systems like maize where *A. bipunctata* lays most of its eggs near large aphid aggregations (Schellhorn and Andow 1999), which are also the aggregation sites of *H. axyridis* adults and later instar larvae (*J.P.H. unpublished data*). The recent findings of *A. bipunctata* in Japan (Sakuratani 1994; Toda and Sakuratani 2006) and *H. axyridis* in the United Kingdom (http://www.harlequin-survey.org/) will allow researchers to look at these and other possible interactions in new environmental settings.

It is not clear how *C. septempunctata* and *H. axyridis* have interacted in regards to their possible effects on *A. bipunctata*. As mentioned, *C. septempunctata* may have been completely responsible for observed population declines. Alternatively, *A. bipunctata* may have been negatively affected by *C. septempunctata* before *H. axyridis* arrived, only to have these effects counterbalanced or replaced by negative effects from *H. axyridis* once it arrived. This could happen, for example, if *H. axyridis* is suppressing *C. septempunctata* (as suggested in Brown 2003). Further research on combined or offsetting effects between these two exotic species may help untangle these possibilities.

Coccinella novemnotata

Evidence for decline

Coccinella novemnotata, hereafter C-9 was believed to be the most commonly collected member of the family Coccinellidae in the Northeastern US (Gordon 1985). According to the literature and field guides, C-9 was found throughout the continental United States and southern Canada (Gordon 1985) and was recognized for its considerable economic importance as a predator of many of the more destructive aphid species (Pack 1925). By the mid-1990s it became obvious that C-9 was no longer as common as everyone assumed that it had been in the 1980s and probably the 1970s. The historically broad geographic range and prominence of C-9 stands in stark contrast to its current distribution (Table 3). Besides published reports, a search of major insect collections in the Northeastern US as well as USDA records revealed that C-9 was not common in the 1980s or early 1990s (Stephens 2002). Based on the latest records in the literature, C-9 was last collected in Maryland in 1986, Pennsylvania in 1987, Delaware in 1988 and Maine in 1992 (Wheeler and Hoebeke 1995). As far as recent collections go, C-9 has been collected in the Midwest and West Coast but only sporadically in these areas. Near Madison, Wisconsin, two C-9 were collected the summer of 2000 on milkweed eating milkweed aphids, *Aphis nerii*. In Washington State near Pullman, several maculate C-9 were collected the summer of 2001. The spotless or immaculate variety of *C. novemnotata* that is the primary phenotype of C-9 on the West Coast was collected in the Pajaro Valley near Santa Cruz, California.

Table 3 Surveys of *C. novemnotata* through time

Time period	Average relative abundance of C9	Total # of studies	# Of studies with C9	Average rank of C9[a]
1914–1964	6.6	13[b]	11	3.1
1973–1989	0.06	8	6	6.5
1990–2006	0	32	0	na

Data here include studies from the full data set that were conducted in areas within C9 published range as well as data from an additional study (Ellis et al. 1999)

[a] Average rank in abundance of C9 among all coccinellids in a system, only includes studies where C9 was present

[b] 5 of 13 references are from a single reference across multiple habitats

From dissertations at Cornell University, one can reconstruct the coccinellid fauna composition around Ithaca, NY in particular, with an additional data point for Long Island, NY. In a sample taken in 1924 in alfalfa in Ithaca, NY C-9 made up 13% of the Coccinellidae collected (Pack 1925). A survey of natural enemies in potato on Long Island, NY from 1956 to 1958 found that C-9 made up 19% of the Coccinellidae collected (Day 1965). By 1971 C-9 was evidently less common in Ithaca, NY in alfalfa and represented by a maximum of only 1 individual counted per weekly 100 stem counts (Wheeler 1971).

Potential reasons for decline

Although the critical time for taking data on this disappearance is obviously past, it is important that we garner what we can from the plight of C-9 because other native coccinellids may also be vulnerable to extinction. As with many rare and endangered species, often extinction has a primary cause like habitat destruction or degradation, but many factors actually act in concert to push the species over the brink. Data can be used to gain insight into two important hypotheses for C-9's disappearance; the succession of farmland and the widespread establishment of adventive species.

The Northeast US has undergone an unprecedented greening in the last 120 years precipitated by succession of agricultural land on a large scale. Although the succession of land is often good for many species, it may mean less favorable foraging for C-9 which may have favored agricultural habitats (Gordon 1985, but see Gagne and Martin 1968). Beginning in the 1880s agricultural land in New York began to be abandoned because it was difficult to farm and required more effort for sub-optimal yields in comparison to the land available in the Midwest and Western U.S. (Williams 1989). There was a 57% reduction in land in farms, a 50% reduction in cropland and a 33% reduction in land in orchards between 1940 and 1997 (U.S.D.A. N.A.S.S.; New York State Agricultural Statistics Service 2001). Also, between 1959 and 1997, the land in two major field crops was reduced drastically; wheat acreage diminished by 50% and potatoes by 68% (U.S.D.A. N.A.S.S.). While these large scale changes in habitat and prey availability suggest a possible explanation, the critical data necessary to demonstrate causality was never collected. Moreover, more recent studies have not found any correlation between a changing landscape in South Dakota and Coccinellid densities (Elliot and Kieckheffer 1990; Elliott et al. 1999)

Many entomologists assume that adventive lady beetles, such as *C. septempunctata* and *H. axyridis* played a role in C-9's disappearance, but there is a lack of studies that document a causal relationship (Wheeler and Hoebeke 1995). The timing of C-9's disappearance in Michigan suggests that *H. axyridis* was not responsible for C-9's decline because C-9 was not showing up in collections before *H. axyridis*' arrival (Colunga-Garcia and Gage 1998). Being a member of the same genus, *C. septempunctata* may have occupied a similar niche as *C. novemnotata* (Gordon 1985) resulting in overlap in the use of habitats and possibly intraguild predation events. These *Coccinella* species had similar developmental times and egg and pupal durations and could therefore overlap temporally in their use of habitats (ElHag and Zaitoon 1996). There is a lack of data around the time of C-9's disappearance and *C. septempunctata's* establishment and no studies that determine the frequency, probability or direction of intraguild predation events. Unless more data are uncovered, it will be impossible to draw any conclusions about adventive species causing C-9's disappearance or of the possibility of other alternative hypotheses.

Summary and conclusions

From our survey of the published literature, it is clear that in just the last 20 years coccinellid assemblages of Canada and the United Stated have shifted from being all native to having some, often times very large, proportion of adventive coccinellid species. Less clear is what effect adventives have had on coccinellids as a whole, their ecological function, and why some systems and species have been more affected by adventives than others.

The few studies that have encompassed a coccinellid invasion demonstrate that the number of natives and the total number of coccinellids have sometimes increased and sometimes decreased following the establishment of adventives (Table 1). While the additional, larger survey is suggestive of a strong directional trend, the use of proportions can sometimes be difficult to interpret. Specifically, some or all of the observed decrease in the proportion of native species could simply be due to the addition of adventive species to the assemblage and not a change in the actual density of natives (as in Elliott et al. 1996 alfalfa & grains). However, our review found that the average proportion of native coccinellids decreased by 68% after 1986. To find this large a decrease in the proportion of natives by only adding adventive coccinellids, adventives would have had to increase the total abundance of coccinellids by more than 50% while having no effect on the number of natives. There is one case where such a large number of adventives were added to the assemblage (Alyokhin and Sewell 2004), yet in this system the large insurgence of adventives coincided with a 72% decrease in the density of natives. It is therefore unlikely that the entire decline in the proportion of native species seen in many assemblages has been due to the simple addition of adventive species. Given the tremendous variation in the proportion of natives observed across assemblages since 1987, we can speculate that there are a number of systems in which adventives had a minor or even positive effect on natives. However, it is likely that some systems, especially those with a small proportion of natives, are additional examples of a coccinellid invasion coinciding with a decrease in the native coccinellid population. Unfortunately, we can infer even less from the larger data set on how total coccinellid populations have been affected and are left to rely on the variable results reported across the small number of long-term studies.

Coccinellids, especially the aphidophagous species that dominate published surveys, are not well known for tightly coupled, evolutionarily derived relationships with specific species or habitats. Therefore, it can be difficult to predict what specific ecological functions have suffered from the diminishing of particular species. There is an obvious inherent risk to the presence of native species, but it is not clear what risks adventives are posing to the ecological services coccinellids provide. In fact there may be evidence that adventives have actually helped coccinellids regulate aphids in managed systems. Two recent studies have documented long-term declines in aphid densities since the establishment of an adventive species (Alyokhin and Sewell 2004; Evans 2004). Moreover, one adventive coccinellid, *H. axyridis*, is regarded as one of the only established natural enemies capable of regulating a major recent adventive pest in North American agriculture (Rutledge et al. 2004). More work is needed throughout native ecosystems to understand what additional risks adventives may pose to coccinellids and their functions in these less well-studied environments.

Our case studies on the decline of *A. bipunctata* and *C. novemnotata* illustrate that at least some species in some systems have recently undergone extensive declines. Additional circumstances such as changing land use practices may have helped exacerbate situations, but in both cases it seems extremely likely that adventive species played a role. What is needed now is a better understanding of why these two species have undergone more substantial changes than other natives. Are there specific characteristics in their physiology, ecology, or habitat use that put coccinellid species more at risk, or are there specific types of habitats, ecosystems, or landscapes that put any species more at risk than others? While these are not new questions to conservation or risk assessment, coccinellid ecology would benefit greatly from the application of these other disciplines' current tools and theories. Current invasions of coccinellids in Europe, Asia, and Australia highlight the need to understand what risks are posed to native coccinellids and what can be done to emasculate the negative effects of adventive species.

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