Lady Beetles in New York: Insidious Invasions, Erstwhile Extirpations, and Recent Rediscoveries

Author(s): John E. Losey, Leslie L. Allee, Erin Stephens, Rebecca R. Smyth, Peter Priolo, Leah Tyrrell, Scott Chaskey, and Leonard Stellwag

Source: Northeastern Naturalist, 21(2):271-284. 2014.
Published By: Eagle Hill Institute
DOI: http://dx.doi.org/10.1656/045.021.0209
URL: http://www.bioone.org/doi/full/10.1656/045.021.0209

Lady Beetles in New York: Insidious Invasions, Erstwhile Extirpations, and Recent Rediscoveries

John E. Losey[1], Leslie L. Allee[1,*], Erin Stephens[1], Rebecca R. Smyth[1], Peter Priolo[2], Leah Tyrrell[1], Scott Chaskey[3], and Leonard Stellwag[1]

Abstract - Over the past 40 years, the complex of coccinellid (lady beetle or ladybug) species in New York has undergone substantial changes. Primarily, these changes have involved the decline of native species and the increase and spread of adventive species. Species declines have proceeded to the extent that several native species were feared to be extirpated from New York. Here we report that two of these native species, *Adalia bipunctata* (Two-spotted Lady Beetle) and *Coccinella novemnotata* (Nine-spotted Lady Beetle), were rediscovered in New York, in 2009 and 2011, respectively, by volunteers and specialists working for the Lost Ladybug Project. We found that the current coccinellid complex in New York is significantly less diverse and has a significantly higher proportion of foreign species compared to the complex in the past. We discuss the potential causes and implications for these shifts and rediscoveries.

Introduction

Coccinellids (lady beetles or ladybugs) are important predators in both natural and agricultural habitats. They provide the ecosystem service of controlling herbivorous insects (Hodek et al. 2012). In agricultural habitats, coccinellids prey on many economically important pests including aphids and other soft-bodied insects (Metcalf et al. 1994). Coccinellids are common and economically important predators in *Zea mays* L. (Corn) agroecosystems, preying upon pests of primary and secondary importance, including aphids and *Ostrinia nubilalis* (Hübner) (European Corn Borer) larvae and eggs (Gordon 1985). In natural areas, coccinellids suppress outbreaks of a variety of herbivores and many species of aphids (Pack 1925). Because coccinellids are vulnerable to limiting factors such as natural enemies, introduced competitors, and other anthropogenic influences, they are recognized as important bioindicators (Iperti 1999).

Numerous studies have examined the composition of the coccinellid complex, and a smaller but no less important body of literature has related their density and diversity to ecological function. Previous work has shown that coccinellid species vary widely in the level of suppression they exert on various prey species (reviewed in Hodek et al. 2012) and in their response to environmental changes (Bazzocchi et al. 2004, Iperti 1999). These findings imply that long-term regional shifts in coccinellid species composition may result in important changes in the functioning of this complex and its response to environmental changes.

[1]Lost Ladybug Project, The Old Insectary, Department of Entomology, Cornell University, Ithaca, NY 14853. [2]82 Chichester Avenue, Center Moriches, NY 11934. [3]Quail Hill Farm, Amagansett, NY 11930. [*]Corresponding author - LLA1@cornell.edu.

Manuscript Editor: Dan Pavuk

Twenty-six of the more than 500 coccinellid species of North America north of Mexico are exotic and were introduced for biological control (Gordon 1985, Hodek et al. 2012). Three of the most successful and widely established introduced coccinellids are *Coccinella septempunctata* (Seven-spotted Lady Beetle), *Propylaea quatuordecimpunctata* (Fourteen-spotted or Checkerspot Lady Beetle), and *Harmonia axyridis* (Multicolored Asian Lady Beetle), which were first established in North America in 1973, 1972, and 1988, respectively (Gordon and Vandenberg 1991). Multicolored Asian Lady Beetle and Seven-spotted Lady Beetle, are active and aggressive predators (Angalet et al. 1973, Cottrell and Yeargan 1998) that are well adapted to disturbed habitats in a variety of climate conditions.

Over the last 30 years, these introduced coccinellid species increased rapidly in both range and density, while several common native species of coccinellids went through dramatic and as yet not well-explained population declines (Harmon et al. 2007, Wheeler and Hoebeke 1995). Adventive coccinellids have been implicated as factors contributing to the decline of native species (Obrycki et al. 2000, Wheeler and Hoebeke 1995). Several studies have documented the propensity of these introduced species to affect the ecology of native species, especially due to intraguild predation (IGP) in the larval stage (Cottrell and Yeargan 1998, Elliot et al. 1996, Obrycki et al. 1998). In contrast, several other studies have shown relatively uniform effects of IGP between native and introduced species (Gagnon et al. 2011, Gardener et al. 2011). Most recently, a secondary mechanism has been proposed by European researchers to explain the success of Multicolored Asian Lady Beetle in Europe and the decline of Seven-spotted Lady Beetle, a species native to Europe, as a result of IGP: Multicolored Asian Lady Beetle is immune to but carries lethal microsporidia that are ingested by the susceptible Seven-Spotted Lady Beetle during IGP (Vilcinskas et al. 2013). While the mechanisms of each species interaction are not yet clear, Harmon et al. (2007) showed that introduced species were making up an increasingly large component of many communities, and that many formerly dominant coccinellids were no longer collected, including *Coccinella novemnotata* (Nine-spotted Lady Beetle), *Coccinella transversoguttata* (Transverse Lady Beetle), *Adalia bipuncatata* (Two-spotted Lady Beetle), and *Hippodamia convergens* Guérin-Méneville (Convergent Lady Beetle). These changes have been a cause for concern because most effective pest suppression comes from a diverse complex of coccinellid species that includes native species (Snyder 2009).

Increased dominance of introduced species and decline of native species have been especially pronounced in the northeastern US (Harmon et al. 2007, Wheeler and Hoebeke 1995). The original range of the native species Nine-spotted Lady Beetle and Two-spotted Lady Beetle included NY and the entire Northeast (Gordon 1985). In 2008, the Lost Ladybug Project (LLP), a citizen-science program designed to recruit volunteers to gather data on the current status of coccinellids in North America, was launched. As of June 2012, the LLP had over 17,000 identified images of individual coccinellids, each of which was connected with collection data. New York is particularly well represented in that database, with over 1400 observations. In this paper, we combine the LLP data with data from Stephens (2002) to elucidate changes in the coccinellid complex in New York and similar changes that have occurred throughout the Northeast US.

Field-Site Descriptions

Volunteers participating in the LLP surveyed Coccinellids across New York. We targeted two areas for increased sampling effort following the rediscovery of rare native species by volunteers at these sites. These two field sites are described below.

The research survey area where Nine-Spotted Lady Beetle was found includes the vegetable and flower plots of Quail Hill Farm, an organic farm in the Long Island town of Amagansett, NY (40°97'36"N, 72°14'42"W). Long Island is in the North Atlantic coastal ecoregion and is characterized by grasslands, shrublands, vast pine barrens, coastal plain ponds, dunes, and extensive salt marshes. This ecoregion differs from more southern coastal ecoregions by having coarser-grained soils and *Quercus* (oak)-*Pinus* (pine) vegetation; it has less flat physiography than the middle Atlantic coastal plain, but is more uniform than the northeastern coastal zone. The main soil type, Bridgehampton silt loam, is well drained and occurs on 0–2% slopes with silty glaciolacustrine or eolian parent material underlain by contrasting glacial drift, derived mainly from gneiss, granite, and schist with some sandstone, conglomerate, and shale. The typical profile is: 0–28 cm silt loam, 28–142 cm silt loam, and 142–203 cm stratified gravelly sand. Average elevation is 9 m. Located in the USDA growing zone 7a (-17 °C to -15 °C annual minimum temperature), this area has a mean annual precipitation of 114–127 cm, a mean annual air temperature of 10–12 °C, and a frost-free period of 150–225 days with the average first frost in mid-November and the average last frost in mid-April.

The research area where surveyors found Two-spotted Lady Beetle is in the residential area surrounding Buffalo State University in Buffalo, NY (42°88'64"N, 78°87'86"W). The Great Lakes ecoregion is glaciated with gently rolling hills and irregular flat lake plains. It has a high level of biodiversity and unique habitats with a climate influenced by the Great Lakes (NYS DEC n.d.). This region differs from the northeastern highlands, northern Appalachian Plateau, and uplands ecoregions because it generally has less surface irregularity and more agricultural activity and population density. Land use in the Lake Erie plain watershed basin surrounding Buffalo is dominated by agriculture associated with dairy operations but also contains orchards, vineyards, and vegetable farms. Because Buffalo is close to Lake Erie, it has an increased growing season, more winter cloudiness, and greater snowfall than surrounding areas. The main soil type, Urban-Churchville complex, has a parent material of clayey glaciolacustrine deposits over loamy till, occurs on 0–3% slopes, and is somewhat poorly drained. The typical profile is: 0–28 cm silt loam, 28–66 cm silty clay, and 66–152 cm gravelly loam. Average elevation is 442 m. Located in the USDA growing zone 6a (-23 °C to -21 °C minimum annual temperature), this area has a mean annual precipitation of 91–122 cm, a mean annual air temperature of 7–10 °C and a frost-free period of 115–195 days, with the average first frost in mid-October and the average last frost in early to mid-May.

Methods

New data for this study was taken from the LLP (http://www.lostladybug.org/), the citizen-science project that documents changing distributions of coccinellids across North America. At the time of this analysis, the LLP had over 17,000 verified records of coccinellids, with over 1400 verified records from New York, and collection has continued since then. LLP protocols direct that volunteers count groups of aestivating coccinellids as single observations of that species because they may not be functionally equivalent to a similar number of active individuals in the field. We compared these data with published data from Pack (1925), Day (1965), and Stephens (2002). Pack (1925) used visual sampling to survey *Medicago sativa* L. (Alfalfa) fields in Ithaca, NY, in 1924; Day (1965) used sweep-net sampling to survey *Solanum tuberosum* L. (Common Potato) fields in Riverhead, NY in 1956–1958; and Stephens (2002) used yellow sticky-card sampling to survey in mixed habitats (natural areas, gardens, and Alfalfa) in multiple locations in 2000–2001. The LLP used visual and sweep-net sampling to survey in mixed habitats (natural areas, gardens, wetlands, shorelines, buildings, agricultural crops—including Alfalfa, Corn, Potato, *Malus* spp. (apple), *Rubus idaeus* L. (Raspberry)—in multiple locations in 2008–2012.

We suspected that the major change reported in coccinellid complexes (Harmon et al. 2007, Wheeler and Hoebeke 1995) was caused by the introduction of two foreign species, Seven-Spotted Lady Beetle and Multicolored Asian Lady Beetle. Thus, we examined each survey separately, and then pooled the two pre-introduction surveys—Pack (1925) and Day (1965)—and the two post-introduction surveys— Stephens (2002) and the 2012 LLP effort—and compared the pooled data as two distinct time periods with methods generally following Stephens et al. (2012). To examine the diversity between pre- and post-introduction time periods, we calculated Simpson's *D* with the formula

$$D = \sum (n / N)^2 ,$$

where n is the number of individuals in a category and N is the total number of all coccinellids collected. To make the values more intuitive, we present $1 - D$ so that low values represent lower diversity and higher values represent higher diversity.

Because pre-introduction surveys were done in single habitats and post-introduction surveys covered multiple habitats, we also compared differences in the diversity index in pre- and post-introduction surveys in a single crop, Alfalfa.

Because diversity indices are not directly quantitatively comparable, we compared diversity between treatments by calculating and statistically comparing the ratio of effective species (Jost 2006). The number of effective species (E) was calculated as $E = 1 / D$. To determine the magnitude of the difference in the number of effective species between time periods, we calculated the ratio of effective species (E_1 / E_2) for each pair of treatments. Pairs with a ratio close to one have a similar number of effective species, while values far from one denote pairs with disparate numbers of effective species. To determine if pairs of treatments differed significantly in their number of effective species we calculated the variance in the proportions (n / N) comprised by the species within a treatment using the formula

$$s^2 = (R[*\sum(n / N)^3] - \sum([n / N]^2)^2) / N,$$

where R = species richness, and then used those variances to perform a t-test.

Results

Among the 29 coccinellid species documented in the surveys (1924–present), several species showed clear changes over time (Table 1). The two most notable are the decrease in collection occurrence of four native species—Two-spotted Lady Beetle, Nine-spotted Lady Beetle, Transverse Lady Beetle, and Convergent Lady Beetle observed with the simultaneous increase in collection occurrence of three exotic species—Seven-Spotted Lady Beetle, Multicolored Asian Lady Beetle, and Fourteen-spotted Lady Beetle.

Of all species collected during the surveys, the native species, Transverse Lady Beetle, showed one of the most marked declines. This was the most commonly collected species in 1924 (ranked 1st) and accounted for 40.0% of the sample. Transverse Lady Beetle represented only 5.0% of 1956–1958 collections, but was still ranked 4th among all coccinellid species in abundance then. Because other studies and surveys also show Transverse Lady Beetle was a constant but variable species across the Northeast before introduction of exotic species, we combined the Pack (1925) and Day (1965) data sets. Transverse Lady Beetle was not recorded in New York in the 2000–2001 or 2008–2012 surveys.

Like Transverse Lady Beetle, Nine-spotted Lady Beetle was an important component of the early surveys, accounting for 13.0% of the sample in 1924 (ranked 4th) and 18.0% between 1956 and 1958 (ranked 2nd). Nine-spotted Lady Beetle was not found in the 2000-2001 survey but LLP surveyors rediscovered it during the 2008–2012 survey where it represented 1.0% of collections (Table 1). Specifically, in July and August 2011, volunteers and specialists working for the LLP discovered over 20 adult Nine-spotted Lady Beetles on Long Island, NY. All the individuals found were uniform with relatively large black spots on dark red elytra (Fig. 1).

The results for Two-spotted Lady Beetle and Convergent Lady Beetle were very similar to the pattern exhibited by Nine-spotted Lady Beetle. Two-spotted Lady Beetle and Convergent Lady Beetle were not found in the 2000–2001 survey but were rediscovered in the 2008–2012 survey, where they represented 0.2 and 0.3% of collections, respectively (Table 1). However, unlike the Nine-spotted Lady Beetle, which has only been found in one Long Island, NY, location, both Two-spotted Lady Beetle and Convergent Lady Beetle have been found in multiple locations in upstate NY as well as downstate. Starting in July 2009, volunteers and specialists working for the LLP found Two Spotted Lady Beetles in a yard, public garden, and park—all organically maintained—in Buffalo, Rochester, and Brooklyn, NY, respectively. All the individuals found were uniform with two large black spots on red elytra (Fig. 2). Starting in 2008, LLP personnel found Convergent Lady Beetles in Woodside, Bayshore, Fairport, and Medina, NY.

All three species—Two-spotted Lady Beetle, Nine-spotted Lady Beetle, and Convergent Lady Beetle—were present in the early surveys, absent in the 2001–2002 survey, and rediscovered in the 2008–2012 survey.

One native species, *Coleomegilla maculata* (Spotted Lady Beetle), revealed a pattern inversely related to the other natives, representing 0.0% of the samples in 1924 and1956–1958, 19.0% in 2000–2001, and 12.0% in 2008–2012.

Three exotic species —Seven-Spotted Lady Beetle, Multicolored Asian Lady Beetle, and Fourteen-spotted Lady Beetle—were not represented in the earliest surveys because they had not yet become established in the US. By the 2000–2001

Table 1. Percentages and ranks (in parentheses) of native and introduced coccinellid species found in four New York surveys conducted in various habitats between 1924 and 2012. * = introduced species.

	Data source			
	Pack 1925	Day 1965	Stephens 2002	2012 LLP data
Crop	Alfalfa	Potatoes	Mixed	Mixed
Year sampled	1924	1956–1958	2000–2001	2008–2012
Species				
Adalia bipunctata L.	2 (7)	3 (7)	0	0.2 (16)
Anatis labiculata (Say)	0	0	0	0.1 (18)
Anatis mali (Say)	0	0	0	0.3 (13)
Anisosticta bitriangularis (Say)	0	0	0	0.1 (21)
Brachiacantha indubitalis (Crotch)	0	0	16 (3)	0
Brachiacantha ursina (Fabricius)	0	0	15 (4)	0.2 (16)
*Chilocorus kuwanae** Sylvestri	0	0	0	0.1 (21)
Chilocorus stigma (Say)	0	0	0	1 (6)
Coccinella novemnotata Herbst	13 (4)	18 (2)	0	1 (6)
*Coccinella septempunctata** L.	0	0	1 (8)	8 (4)
Coccinella transversoguttata Brown	40 (1)	5 (4)	0	0
Coccinella trifasciata L.	11 (5)	2 (9)	0	1 (6)
*Coccinella undecimpunctata** L.	0	52 (1)	0	0
Coleomegilla maculata DeGeer	0	0	19 (2)	12 (2)
Cycloneda munda Say	0	5 (4)	3 (6)	1 (6)
Diomus terminatus (Say)	0	3 (7)	0	0
*Epilachna varivestis** Mulsant	0	0	0	0.2 (14)
*Harmonia axyridis** (Pallas)	0	0	34 (1)	59 (1)
Hippodamia convergens Guerin	15 (2)	9 (3)	0	0.3 (12)
Hippodamia glacialis (Fabricius)	0	0	0	1 (6)
Hippodamia parenthesis (Say)	15 (2)	0	2 (7)	1 (6)
Hippodamia tredecimpunctata (L.)	3 (6)	4 (6)	0	0
*Hippodamia variegata** (Goeze)	0	0	0	2 (5)
Hyperaspis binotata (Say)	0	0	0	0.1 (18)
Hyperaspis signata Olivier	0	0	0	0.1 (18)
Neoharmonia venusta (Melsheimer)	0	0	0	0.2 (14)
Olla v-nigrum (Mulsant)	0	0	0	0
*Propylaea quatuordecimpunctata** L.	0	0	11 (5)	11 (3)
Psyllobora vigintimaculata (Say)	0	0	0	0.1 (21)
Total *n*	67	105	296	1458
Species richness	7	9	8	23
Simpson's *D*	0.78	0.68	0.79	0.62

Figure 1. The single individual that comprised the initial discovery in July 2011 of the first *Coccinella novemnotata* (Nine-spotted Lady Beetle) seen in New York in 29 years.

Figure 2. The single individual that comprised the initial discovery in July 2009 of the first Two-spotted Lady Beetle, *Adalia bipunctata,* seen in New York in 24 years.

survey, these foreign species represented 46.0% of all species and they represented 78.0% of all species in the 2008–2012 survey. Multicolored Asian Lady Beetle was the most common species in both of the recent surveys.

One exotic species exhibited a different pattern: *Coccinella undecimpunctata* (Eleven-spotted Lady Beetle) represented 52.0% of the surveyed population between 1956 and 1958 but did not occur in any other of the three surveys.

Table 2. Comparison of coccinellid complexes in pooled New York surveys, pre- and post-introduction of three exotic coccinellid species: *Coccinella septempunctata*, *Harmonia axyridis*, and *Propylaea quaturodecimpunctata*. Differences between numbers of effective species and between percent of introduced species were compared using *t*-tests ($P < 0.05$).

	Pre-introduction (Pack 1925, Day 1965)	Post-introduction (Stephens 2001; 2012 LLP data)
Total individuals (*N*)	165	1755
Species richness (S)	9	26
Diversity index (1 - *D*)	0.82	0.67
Effective species (E)	5.4a	3.0b
Percent introduced species	33%a	74%b

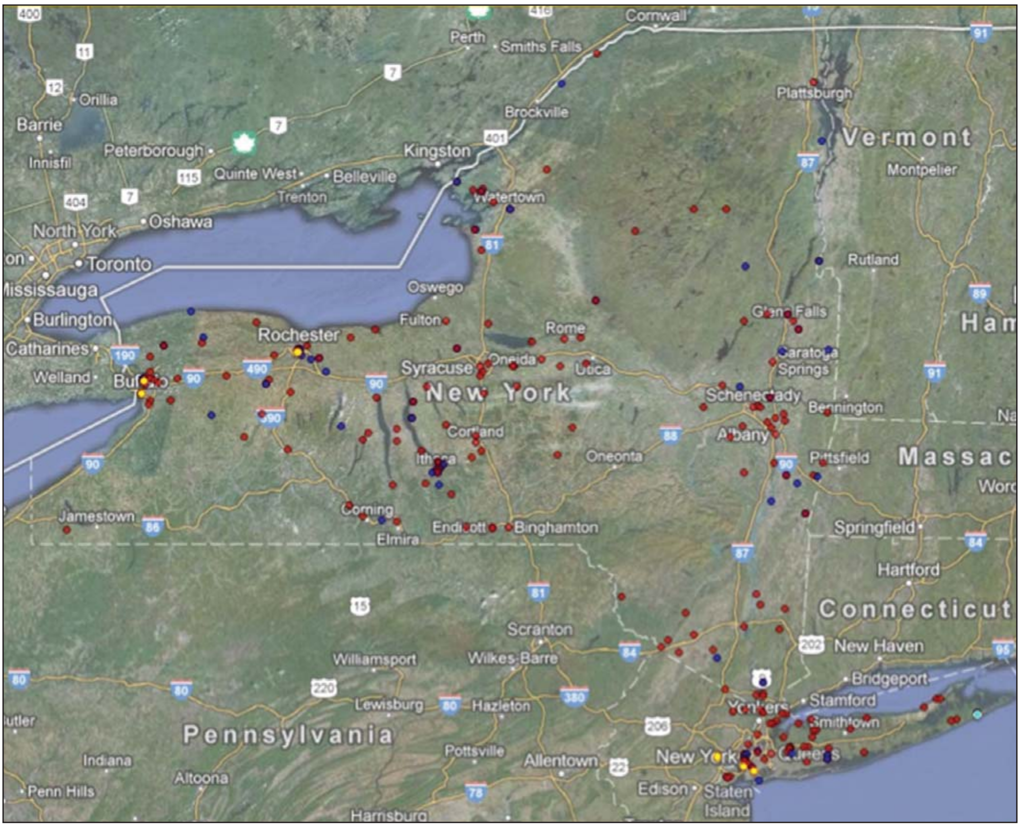

Figure 3. Map of all lady beetle observations in New York by the Lost Ladybug Project 2008–2012 with introduced species in red, and native species *C. novemnotata* in green, *A. bipunctata* in yellow, and all other native species in blue.

The diversity indices for the four surveys ranged from 0.79 to 0.62, with each period (pre- and post-establishment of major foreign species) having one relatively high and one lower diversity rating (Table 1). The pooled pre-introduction surveys had a higher diversity index (0.82) than the pooled surveys from the post-introduction time period (0.67) even though species richness was lower (9 and 26, respectively; Table 2). When we compared post- and pre-introduction-periods collections from a single crop, the diversity index for coccinellids surveyed in Alfalfa in 2001 (0.65; Stephens 2002) was substantially lower than the index for coccinellids surveyed in 1924 (0.78; Pack 1925).

Differences in this or any diversity index can be difficult to interpret, but the number of effective species (E) in the pre-introduction period (5.4) was also significantly higher than the number in the post-introduction period (3.0; $P < 0.001$; Table 2) with a pre- to post-introduction ratio of 0.55 for effective species. This decrease in the number of effective species corresponded with a significant increase of the dominance of foreign species, which increased from 33.0% in the pre-introduction time period to 74.0% in the post-introduction period ($P = 0.001$; Table 2).

Results from the LLP's 2008–2012 survey added to our knowledge about the current status of the coccinellid complex in NY (Fig. 3). Our data show that the coccinellid complex in NY is composed of 78% foreign ladybugs, dominated by Multicolored Asian Lady Beetle, and 22% native ladybugs, dominated by Spotted Lady Beetle; we detected native Two-spotted Lady Beetle and Nine-spotted Lady Beetle only rarely.

Discussion

One of the major patterns in the coccinellid complex in NY has been the disappearance and rediscovery of several native species. These species were present and, in many cases, they were substantial components of the coccinellid complex of New York up to 50 years ago, but by 2000 they were notably absent. Using the Cornell University Insect Collection (CUIC), it was possible to determine more precisely when these species were last seen in New York within the period 1958–2000. The latest dated specimens in the CUIC were 1980, 1982, and 1985 for Transverse Lady Beetle, Nine-spotted Lady Beetle, and Two-spotted Lady Beetle, respectively. The same pattern of disappearance has been shown across the Northeast. The most recent survey of northeastern North America to detect Nine-spotted Lady Beetle was in 1982, and 6 subsequent surveys from 1993 to 2001 in various northeastern states and provinces did not record this species (Losey et al. 2007).

Some native species have disappeared and have not yet been rediscovered. Despite a multi-location survey in 2001 and extensive sampling by LLP volunteers across NY—including over 1400 coccinellids documented from 2008–2012—Transverse Lady Beetle, has not been rediscovered in NY. The same is true for the Northeast as a whole; other research studies document that Transverse Lady Beetle was a common but variable species in the Northeast prior to the introduction of exotic coccinellid species. For example, during 1942–1971 in Maine potato fields, Transverse Lady Beetle ranged in percent of the total coccinellid population from

5.7 to 66.0 (Shands et al. 1972), and Storch (1973) referred to Transverse Lady Beetle as usually the most abundant predator in Maine Potato fields. Yet from 2008–2012, no Transverse Lady Beetles have been found by LLP volunteers in Maine or any other northeastern state. Based on the surveys we examined, it appears that at least one other species has disappeared from New York as well. Although we know very little about its relative abundance, the CUIC has collection records of *Coccinella hieroglyphica* L. (Hieroglyphic Lady Beetle) from as late as 1949, but we did not observe it during our surveys.

Although the patterns are clear, it is not possible to determine if species like Nine-spotted Lady Beetle and Two-spotted Lady Beetle were extirpated from New York for a period of time between their last collection and then they were rediscovered between 2008–2012 by the LLP or if they were always present at a low density but were just not detected by interim surveys. The latter seems more likely based on 1) both species still appearing to be at low enough densities that they could easily have been missed, 2) the relatively small geographic area covered by the 2000–2001 survey, and 3) the low level of sampling in the Lake Ontario coastal region, where Two-spotted Lady Beetle was rediscovered, and the Long Island region where Nine-spotted Lady Beetle was rediscovered. The type of small, widely dispersed volunteer surveys employed by the LLP has been shown to be more effective at detecting rare species than more concentrated surveys (Losey et al. 2012a). Participants in the LLP surveyed a wide variety of locations across New York, and the breadth of these surveys resulted in the rediscovery of the two rare native species (Fig. 3).

Several hypotheses have been proposed to explain the decline of native coccinellid species in the Northeast, and most encompass negative interactions with introduced coccinellid species. Wheeler and Hoebeke (1995) were among the first to point out the coincidence of the decline of the native Nine-spotted Lady Beetle with the establishment and spread of non-native Seven-Spotted Lady Beetle. A more recent study demonstrated a decrease in the average body size of recently field-collected Nine-spotted Lady Beetles compared to historical specimens across multiple geographical locations and a broad time period (Losey et al. 2012b). This finding is consistent with the hypothesis that foreign species are outcompeting native species for prey. An earlier study found no decline in body size in five other native species and suggested that IGP or habitat compression might be causing the decline of these native coccinellid species (Evans 2000). However, the study occurred in a single geographical crop location, over a much shorter time-span than Losey et al. (2012b), and most importantly, Nine-spotted Lady Beetle was not included because it occurred in insufficient numbers (E. Evans, Utah State University, Logan, UT, pers. comm.). Although further studies of historical records and additional geographically wide field surveys are needed on other native species to further understand the role of competition for prey in their overall decline, it appears that foreign species are at least playing some role, and perhaps a variety of roles, in the decline of native species.

Another interesting finding may, upon further study, help to explain the decline of native coccinellid species in the Northeast. In contrast to the Nine-spotted Lady

Beetles submitted to the LLP by citizen scientists from western states, which were variable and often dominated by individuals with very small black spots on peach or adobe colored elytra, all the individuals found in NY were uniform with relatively large black spots on dark red elytra. Similarly, all the individuals of Two-spotted Lady Beetle found in NY were uniform with two large black spots on red elytra, while other populations contain individuals with no spots, four spots, and a reverse or melanic form. Further study may reveal that specific differences in these and other traits are linked to differences in survival. Differences in coccinellid coloration have been linked to variation in several chemical compounds and subsequent defense against predation by birds (Blount et al. 2012). Differences in coccinellid spot size or melanized surface area have been linked to differences in fitness and to changes in climate (de Jong and Brakefield 1998).

It is important to note that several species are not following the patterns in population changes described above. Notably Spotted Lady Beetle is a native species that is thriving and perhaps even increasing its relative density. One possible explanation for the continuous survival of Spotted Lady Beetle is that it is facultatively pollenivorous, while most other species in the coccinellinae are obligate predators (Michaud and Grant 2005). No such obvious explanation presents itself for Eleven-spotted Lady Beetle (Wheeler and Hoebeke 2008). This was the most common species found in the 1956–1958 survey, but it was not seen in our surveys, although there is one 1982 specimen at CUIC. It seems plausible that conditions allowed this foreign species to flourish for a time—it was first documented in the region in 1912 (Gordon 1985)—but then something changed in the environment that resulted in population decreases (Baltz and Moyle 1993).

Beyond individual species, it is important to consider patterns for the coccinellid complex as a whole. From our calculations of Simpson's diversity index, it does not appear that there is a substantial difference in diversity between the pre-introduction surveys (1924 and 1956–58) and the post-introduction surveys (2001 and 2008–2012; see Table 1). However, one difference between the pre- and post-introduction survey protocols may serve to mask an important pattern. Both pre-introduction surveys were conducted in a single type of habitat, but the post-introduction surveys were conducted across multiple habitats. This is likely an important factor because coccinellid complexes differ across habitats, so combining habitats may obscure the actual diversity of a specific habitat and how it has changed over time. The 2000–2001 survey explains this phenomenon. We conducted our survey across three habitats: natural areas, gardens, and Alfalfa fields. The pooled diversity index, 0.80, is substantially higher than the averaged diversity index calculated using the index value for each specific habitat (0.71). Because the 2000–2001 and 1956–1958 surveys included Alfalfa, it was possible to compare diversity between pre- and post-introduction populations in a single habitat. The result supports our overall conclusion that species diversity has declined with the introduction of coccinellids and the subsequent decline of native species.

To further elucidate the differences between pre- and post-introduction coccinellid complexes, we can pool the two pre-introduction surveys and compare them to the two post-introduction surveys. The results of this comparison show some important differences between the two complexes (Table 2). First, we have many more samples from the post-introduction era (1755) compared to the pre-introduction era (165). This higher level of sampling likely contributed to greater species richness in the post-introduction complex compared to the pre-introduction complex. Even with the greater species richness, the diversity index for the post-introduction complex is substantially lower than the index for the pre-introduction complex. Although diversity indices give a useful single measure of diversity, it can be difficult to interpret differences between diversity indices across space or time (Jost 2006). One practical alternative is to calculate effective species (Jost 2006). This method yields a value that is directly and statistically comparable between two time periods. One useful way to interpret these values is to assess the ratio of the number of effective species across two sets of conditions. A ratio close to 1 indicates very similar diversity, and ratios far from 1 indicate major differences in diversity. Our pre- and post-introduction numbers of effective species yield a ratio of 0.55, which indicates New York has lost nearly half of the diversity in its coccinellid complex following the introduction of major foreign species. We suspect this lowered diversity has been caused by the measurable increase in the dominance of foreign coccinellid species.

The decline of native coccinellid species in New York over the last several decades is cause for concern, particularly because a diverse complex of coccinellids that includes native species has been shown to provide the most effective pest suppression (Snyder 2009). However, recent rediscoveries have demonstrated that although many of the native species have become rare, they are not extirpated in New York. The confirmation of these species in the same locations over several seasons offers hope that they are viable populations that may persist and potentially even expand to provide more balance with introduced species. Long-term citizen-science surveys such as the LLP are particularly well suited to provide the type of data needed to monitor these changes. Beyond determining the impact on coccinellid species themselves, this system can serve as a model for predicting the impact of other invasive species on the natural history of the Northeast.

Acknowledgments

The authors wish to thank the Quail Hill Farm 2011–2013 field crews for their enthusiastic assistance. The authors also thank the Peconic Land Trust for their gracious hospitality and support. The LLP is funded by a grant from the Informal Science Education Program of the National Science Foundation.

Literature Cited

Angalet, G., and R. Jacques. 1973. USDA. Cooperative economic insect report. Newark, DE. 883–884 pp.

Baltz, D.M., and P.B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications 3:246–255.

Bazzocchi, G.G., A. Lanzoni, G. Accinelli, and G. Burgio. 2004. Overwintering, phenology, and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. BioControl 49:245–260.

Blount J., H. Rowland, F. Drijfhout, J. Endler, R. Inger, J. Sloggett, G. Hurst, D. Hodgson, and M. Speed. 2012. How the ladybird got its spots: Effects of resource limitation on the honesty of aposematic signals. Functional Ecology 26:1–9.

Cottrell, T.E., and K.V. Yeargan. 1998. Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). Journal of the Kansas Entomological Society 71:159–163.

Day, W.H. 1965. The identification and importance of biotic and abiotic factors affecting aphids on Long Island potatoes. Ph.D. Thesis. Cornell University, Ithaca, NY. 420 pp.

de Jong, P.W., and P.M. Brakefield. 1998. Climate and change in clines for melanism in the Two-Spot Ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). Proceedings: Biological Sciences 265:39–43.

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

Evans, E.W. 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.

Gagnon, A.E., G.E. Heimpel, and J. Brodeur. 2011. The ubiquity of intraguild predation among predatory arthropods. PLoS ONE 6:e28061.

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

Gordon, R.D. 1985. The Coccinellidae (Coleoptera) of America North of Mexico. Journal of the New York Entomological Society 93:1–912.

Gordon, R.D., and N. Vandenberg. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. Proceedings of the Entomological Society of Washington 93:845–864.

Harmon, J.E., J. Stephens, and J. Losey. 2007. The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. Journal of Insect Conservation 11:85–84.

Hodek, I., A. Honek, and H.F. van Emden. 2012. Ecology and Behavior of the Ladybird Beetles (Coccinellidae). Wiley-Blackwell, New York, NY. 600 pp.

Iperti, G. 1999. Biodiversity of predaceous coccinellidae in relation to bioindication and economic importance. Agriculture, Ecosystems and the Environment 74:323–342.

Jost, L. 2006. Entropy and diversity. Oikos 113:363–375.

Losey, J., J. Perlman, and E. Richard Hoebeke. 2007. Citizen scientist rediscovers rare Nine-spotted Lady Beetle, *Coccinella novemnotata,* in eastern North America. Journal of Insect Conservation 11:415–417.

Losey, J.E., L. Allee, and R. Smyth. 2012a. The Lost Ladybug Project: Citizen spotting surpasses scientist's surveys. American Entomologist 58:22–24.

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

Metcalf, R.L., and W.H. Luckman. 1994. Introduction to Insect Pest Management. Wiley, New York, NY. 650 pp.

Michaud, J.P., and A.K. Grant. 2005. Suitability of pollen sources for the development and reproduction of *Coleomegilla maculata* (Coleoptera: Coccinellidae) under simulated drought conditions. Biological Control 32:363–370.

New York State Department of Environmental Conservation (NY DEC). No date. Natural history of New York State. p. 20. Available online at http://www.dec.ny.gov/docs/wildlife_pdf/nathist.pdf. Accessed May 2014.

Obrycki, J.J., K.L. Giles, and A.M. Ormord. 1998. Interactions between an introduced and an indigenous coccinellid species at different prey densities. Oecologia 117:279–285.

Obrycki, J.J., N.C. Elliot, and L.G. Giles. 2000. Coccinellid introductions: Potential for and evaluation of nontarget effects. Pp. 127–145, *In* P.A. Follett and J.J. Duan (Eds.). Nontarget Effects of Biological Control Introductions. Kluwer Academic Publishers, Norwell, MA. 316 pp.

Pack, H.J. 1925. A biological study of certain ladybird beetles (Coccinellidae). Ph.D. Dissertation. Cornell University, Ithaca, NY. 157 pp.

Shands, W.A., G.W. Simpson, H.E. Wave, and C.C. Gordon. 1972. Importance of arthropod predators in controlling aphids on Potatoes in northeastern Maine. Life Sciences and Agriculture Experiment Station Technical Bulletin 54. 49 pp.

Snyder, W. 2009. Coccinellids in diverse communities: Which niche fits? Biological Control 51:323–335.

Stephens, E.J. 2002. Apparent extirpation of *Coccinella novemnotata* in New York State: Optimizing sampling methods and evaluating explanations for decline. M.Sc. Thesis. Cornell University, Ithaca, NY. 63 pp.

Stephens, E.J., J.E. Losey, L. Allee, A. DiTommaso, C. Bodner, and A. Breyre. 2012. The impact of Cry 3Bb1 *Bt*-maize on two guilds of beneficial beetles. Agriculture, Ecosystems and Environment 156:72–81.

Storch, R.H. 1973. The effect of photoperiod on *Coccinella transversoguttata* (Coleoptera:Coccinellidae). Entomologia Experimentalis et Applicata 16:77–82.

Vilcinskas, A., K. Stoecker, H. Schmidtberg, C.R. Röhrich, and H. Vogel. 2013. Invasive Harlequin Ladybird carries biological weapons against native competitors. Science 340:862–863.

Wheeler, A.G., Jr., and E.R. Hoebeke. 1995. *Coccinella novemnotata* in northeastern North America: Historical occurrence and current status (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington 97:701–716.

Wheeler, A.G., Jr., and E.R. Hoebeke. 2008. Rise and fall of an immigrant lady beetle: Is *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) still present in North America? Proceedings of the Entomological Society of Washington 110:817–823.