Abundance of Native and Non-Native Lady Beetles (Coleoptera: Coccinellidae) in Different Habitats in Maine

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ABSTRACT Several studies suggest the possibility that non-native lady beetles may have replaced native lady beetles in some agricultural habitats. There is relatively little information, however, about lady beetle species composition outside of agricultural habitats. Evans (2004) suggested that native species have retreated to nonagricultural habitats in response to the arrival of non-native lady beetles (habitat compression hypothesis). To test this hypothesis, a survey of lady beetles was conducted in 2004 and 2005 in different habitats in Maine. From May to October, lady beetles were sampled in a variety of agricultural and nonagricultural habitats. In total, 3,487 and 2,903 lady beetles were collected in 2004 and 2005, respectively. Non-native lady beetles were found in a variety of habitats, including the habitats that would have likely served as a refuge for native species if the habitat compression hypothesis applied to the surveyed areas. Native species were found in a higher proportion in agricultural habitats compared with nonagricultural habitats and in very low numbers in all of the habitats surveyed. *Hippodamia tredecimpunctata tibialis* (Say) and *Coccinella transversoguttata* Brown, the two native species that were once dominant here, made up only 1.09 and 0.07% of the total lady beetles collected, respectively. In this survey, we failed to detect evidence that native lady beetles have retreated to nonagricultural habitats in response to the arrival of non-native lady beetles.

KEY WORDS invasive, agricultural, biological control, conservation, aphidophagous

Lady beetles are generally considered beneficial insects because they feed on the pests of crops, including aphids; scale insects; thrips; mites; immature stages of Coleoptera, Lepidoptera, and Hymenoptera; fungi; and weed pollen (Hodek 1973, Gordon 1985). As a result, lady beetles have been intentionally introduced into new habitats throughout the world for the control of agricultural crop pests (Gordon 1985, Koch 2003, Koch and Galvan 2008). Unintentional introductions have also occurred via transport as stowaways in plant exports and other cargo (Chantal 1972, Schaefer et al. 1987, Day et al. 1994). With the increasing concern about the effects of invasive species on native ecosystems, non-native lady beetles (i.e., adventive, introduced, or exotic), which often establish populations in geographical ranges already inhabited by one or more native (i.e., indigenous) or non-native lady beetle species, have been receiving increased scrutiny. In addition to outcompeting other lady beetles for food items (Michaud 2002), non-native species also may prey upon other lady beetle species (Dixon 2000, Yasuda et al. 2004). As a result, introductions of non-native lady beetles have been correlated with reductions in numbers of native lady beetles (Elliott et al. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Brown 2003, Turnock et al. 2003, Alyokhin and Sewell 2004).

Of the 51 lady beetle species currently documented to occur in Maine (Gordon 1985, Bourque et al. 2005), the following seven are non-native: *Coccinella hieroglyphica kirbyi* Crotch, *Stethorus punctum* (LeConte), *Stethorus punctillum* (Weise), *Epilachna varivestis* Mulsant (Mexican bean beetle, an herbivorous pest species), *Hippodamia variegata* (Goeze), *Harmonia axyridis* (Pallas), *Coccinella septempunctata* L., and *Propylea quatuordecimpuncata* L. (Gordon 1985). Relatively little is known about their impact on native lady beetles. Alyokhin and Sewell (2004) evaluated lady beetle populations in potato plots on the Aroostook Research Farm in northern Maine from 1971 to 2001. They reported that until 1980, the dominant lady beetles were the two native species *Hippodamia tredecimpunctata tibialis* (Say) and *Coccinella transversoguttata* Brown, but after *C. septempunctata* became established in 1980, it rapidly became the dominant species and densities of the two native species decreased significantly. With the appearance of *H. axyridis* (1995) and *P. quatuordecimpuncata* (1996), the relative abundances of *H. tredecimpunctata* and *C. transversoguttata* continued to decrease. *H. axyridis* and *P. quatuordecimpunctata* populations increased until 2001 (the last year of the study), perhaps signi-

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Table 1. Locations and habitats of sampling where five yellow sticky cards were deployed throughout each sampling season for 2-wk periods

Habitat	Location[a]						Dominant vegetation
	FR	LT	RF	CR	PI	AF	
Apple			04/05				*Malus* sp., *Elytrigia repens*, *Taraxacum* sp.
Coniferous forest		04/05		04			*Picea* sp., *Pinus* sp., *Abies* sp.
Deciduous forest		04/05				04/05	*Acer* sp., *Betula* sp.
Field		04/05	04	04	05	04/05	*Phleum pratense*, *Trifolium* sp., *Cirsium* sp., *Vicia* sp., *Fragaria* sp.
Grain			04/05			04/05	*Hordeum* sp., *Avena* sp.
Mixed forest	05	04/05	04/05	04	05	04/05	*Acer* sp., *Abies* sp., *Thuja* sp., *Picea* sp., *Betula* sp., *Fagus* sp.
Mixed organic crops			04				*Solanum lycopersicon*, *Allium* sp., *Brassica* sp., *Pisum* sp., *Phaseolus* sp.
Potato	05		04/05			04/05	*Solanum tuberosum*
Riparian		04/05	04/05	04		04/05	*Alnus* sp., *Onoclea sensibilis*, *Cornus sericea*, *Impatiens capensis*, *Mentha* sp.
Shrub	05	04/05		04		04/05	*Solidago* sp., *Rubus* sp., *Prunus* sp., *Rosa* sp., *Cornus sericea*, *Alnus* sp.

Sampling season: In 2004 (04), cards were collected and replaced during the weeks of 17 May, 31 May, 14 June, 28 June, 12 July, 26 July, 9 August, 23 August, 6 September, 20 September 4 October, and 18 October. In 2005 (05), cards were collected and replaced during the weeks of 30 May, 13 June, 27 June, 11 July, 25 July, 8 August, 22 August, and 5 September. Boxes with horizontal and vertical lines represent habitats where five traps were deployed in both 2004 and 2005.

[a] Location abbreviations: FR, commercial potato farm, Fryeburg, ME; LT, Orono Land Trust Land, Orono, ME; RF, University of Maine's Rogers Farm, Orono, ME; CR, commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, ME; PI, rural residential property, Presque Isle, ME; and AF, University of Maine's Aroostook Research Farm, Presque Isle, ME.

fying a shift in dominance as the two, newly established non-native species increased in number. Dominance was then shared by the three non-native species, with the two native species making up <15% of the lady beetle community. Similarly, a 1998 survey in Cape Breton, Nova Scotia, found native lady beetle species, *Coccinella trifasciata perplexa* Mulsant and *Adalia bipunctata* (L.), greatly outnumbered by non-native species *C. septempunctata*, *P. quatuordecimpunctata*, and *H. variegata* (Cormier et al. 2000).

Evans (2004) documented abundances of a non-native lady beetle species (*C. septempunctata*), several native lady beetle species, and their prey [pea aphids, *Acyrthosiphum pisum* (Harris)] in alfalfa, *Medicago savita* L., in Utah in 1992–1994 and 1997–2001. Throughout the course of the study, pea aphid and native lady beetle abundance decreased as *C. septempunctata* abundance increased. Evans (2004) suggested that the reduction in prey density caused by the non-native lady beetle led to a concurrent reduction in native lady beetle abundance. Evans (2004) then artificially enhanced natural populations of pea aphids in an alfalfa field where a reduction in native species had previously coincided with an increase in non-native lady beetles. Native lady beetle abundance increased with increased pea aphid density. Based on this evidence, Evans (2004) suggested that native species have retreated from alfalfa fields to other habitats in response to the depletion of their food resources by *C. septempunctata* but returned when prey species became more abundant. Therefore, in some cases, native species may still dominate in nonagricultural habitats while being replaced by non-native lady beetle species in agricultural ecosystems. This model of resource partitioning and optimal feeding is known as the "compression hypothesis" (MacArthur and Pianka 1966, MacArthur and Wilson 1967). To test this hypothesis, a survey of lady beetles was conducted in 2004 and 2005 in different habitats in Maine to determine whether non-native lady beetle species have replaced native species in a variety of habitats.

When examining lady beetle populations in alfalfa microlandscapes representing habitat loss, fragmentation, and isolation, Zaviezo et al. (2006) did not find differences in where native and non-native lady beetles were found. However, a mounting number of studies document greater abundances of non-native lady beetles compared with native lady beetles in a variety of geographic areas (Wheeler and Hoebeke 1995, Elliott et al. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Turnock et al. 2003, Brown 2003, Alyokhin and Sewell 2004, Evans 2004), their focus almost exclusively on agricultural habitats. Little is known about lady beetle species composition in other habitats.

Materials and Methods

Study Area. Lady beetles were sampled in a variety of habitats (Table 1) at six locations across the state of Maine: commercial potato farm, Fryeburg, ME (FR) (44.0560° N, 70.9801° W); Orono Land Trust Land, Orono, ME (LT) (44.8974° N, 68.6873° W); the University of Maine's Rogers Farm, Orono, ME (RF) (44.9311° N, 68.6937° W); commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, ME (CR) (46.2743° N, 67.8693° W); on rural residential property, Presque Isle, ME (PI) (46.5889° N, 68.0704° W); and the University of Maine's Aroostook Research Farm, Presque Isle, ME (AF) (46.6528° N, 68.0109° W). Habitats at each location were situated within close proximity to each other. For logistical reasons, not all habitats were sampled during both years of the study.

Sampling Protocol. Determination of the best sampling method was based on information in the literature and validated by our comparisons. In a comparison of the success of different methods in sampling coccinellids in alfalfa, Stephens and Losey (2004) found that when yellow sticky cards were deployed for >10 d, they exceeded visual observation and sweep net sampling in the number of coccinellids collected per minute effort. In a 2-yr continuous study by Parajulee and Slosser (2003), yellow sticky cards were more efficient and effective in capturing coccinellids in cotton compared with a two-cycle vacuum sampler. Mensah (1997) found that of a variety of differently colored sticky cards, *Coccinella transversalis* (F.) and *A. bipunctata* in cotton, *Gossypium hirsutum* L., were attracted the most to those that were yellow, suggesting that yellow light in the range of 500 to 580 nm attracted these species the most because this is the range reflected the most by green foliage, where prey is typically found. Our preliminary investigations determined that yellow sticky traps did not bias lady beetle samples compared with net sweeps, beating sheets, and visual observations, but were dramatically more productive and labor-efficient (unpublished data). Based on previous studies, our preliminary data, and the ability to place cards at many locations over long periods, we limited our study to coccinellids collected by yellow sticky cards. We chose to situate cards both in proximity to the ground and to vegetation, as our objective was to determine which coccinellid species were associated with different habitat types. Additionally, previous studies have shown that traps located closer to the ground are more effective in capturing coccinellids (Mensah 1997, Parajulee and Slosser 2003).

Samples were collected continuously from 17 May to 18 October 2004 and from 30 May to 5 September 2005. Five, 15.24- by 30.48-cm yellow sticky strips (Olson Products, Medina, OH) with adhesive on both sides were deployed in each habitat in each location. Trap locations were determined randomly and spaced at least 50 m apart within ≈1–2 ha (agricultural) and >2 ha (nonagricultural) habitats. The cards were hung on stakes or directly from vegetation as close to foliage as possible without sticking to it; thus, the height of cards varied depending on vegetation structure. Cards were deployed in the same location unless changes in vegetation (i.e., growth, senescence) necessitated their vertical movement. Cards were replaced every 2 wk at approximately the same time each day, with each location visited 1 d every 2 wk (ex., Rogers Farm on Tuesday, 14 June; then Tuesday, 28 June, etc.). Cards were then brought to the laboratory and stored in the refrigerator. Captured lady beetles were removed from the traps and identified to species (Gordon 1985). Identifications were later confirmed by Donald Chandler (University of New Hampshire). Voucher specimens of each species were deposited in the Maine Forest Service Insect Collection in Augusta, ME.

Statistical Analyses. The main focus of this study was based upon the assumption that non-native species establishment affects native populations. Therefore, analyses were limited to the lady beetle species with overlapping primary prey items (aphids) and three lady beetle species have been excluded from the analyses: *Psyllobora vigintimaculata* (Say) (a mildew-feeder), *E. varivestis* (a plant-feeder), and *Scymnus* sp. (feeding primarily on scale insects).

The data collected throughout the season were pooled for each trap position. For example, data were pooled from the 12 traps deployed throughout the 2004 season at the LT location in field habitat in position one. Similarly, data from the 12 traps deployed in field habitat at the LT location in position 2 were pooled; and so on, for locations 3, 4, and 5. Thus, there were five trap positions in each habitat in each location where data were collected throughout each season.

Data normality was tested using the Wilk–Shapiro test (PROC UNIVARIATE, SAS Institute 2002). Count data that were not normally distributed were transformed using $\sqrt{X} + 0.001$ transformations (Zar 1999). Means and standard errors reported in this article were calculated from the untransformed data. To compare abundance of native and non-native lady beetles in different habitats, we used a two-way analysis of variance (ANOVA) (PROC GLM, SAS Institute 2002). Analyses were conducted separately for each location during each year of the study. Lady beetle origin (native or non-native) and habitat were used as the main effects. Different lady beetle species were pooled. When an interaction between beetle origin and habitat was statistically significant, we conducted additional paired *t*-tests (PROC TTEST, SAS Institute 2002) comparing mean numbers of native beetles with non-native beetles within each habitat at that location. To determine whether native and non-native species had similar habitat preferences, we used correlation analysis (PROC CORR, SAS Institute 2002) to compare their abundances in different habitats, where the same habitat types in different locations were considered separately.

Results

In total, 3,487 lady beetles were collected in 2004 and a total of 2,903 lady beetles were collected in 2005. Mean numbers of each species captured in each habitat in each location are provided in *Appendix* 1. *P. quatuordecimpuncata*, *H. axyridis*, and *C. septempunctata* were the most numerous non-native species. Three other non-native species also were collected but in very small numbers: *Coccinella hieroglyphica kirbyi*, *E. varivestis*, and *H. variegata*. Lady beetles collected that were native to the region were *Psyllobora vigintimaculata*, *Coleomegilla maculata lengi* Timberlake, *C. trifasciata*, *Hyperaspis* sp., *Hippodamia parenthesis* (Say), *H. tredecimpunctata*, *Mulsantina* sp., *Scymnus* sp., *Chilocorus* sp., *A. bipunctata*, *Anisosticta bitriangularis* (Say), *C. transversoguttata*, *Hippodamia convergens* Guérin-Méneville, *Calvia quat-*

Table 2. Mean ± SE number of aphidophagous lady beetles collected by yellow sticky cards (*N* = 5) throughout the sampling season in each habitat at each location in 2004 and 2005

Location[a]	Habitat	Native no.	SE	Non-native no.	SE	Total no.	SE
2004							
CR	Coniferous forest	1.20	0.8000	0.00	0.0000	1.20	0.8000
	Field	2.20	1.1136	2.40	1.9391	4.60	2.9933
	Mixed forest	0.60	0.2449	1.00	1.0000	1.60	1.1225
	Riparian	1.80	1.1136	6.80	2.8879	8.60	3.0100
	Shrub	2.20	1.2410	4.20	1.2806	6.40	1.6613
LT	Coniferous forest	0.20	0.2000	0.00	0.0000	0.20	0.2000
	Deciduous forest	0.40	0.2449	0.60	0.4000	1.00	0.4472
	Field	11.00	0.4472	35.80	3.3377	46.80	3.0067
	Mixed forest	0.40	0.4000	0.40	0.2449	0.80	0.3742
	Riparian	0.40	0.4000	5.00	2.5495	5.40	2.9428
	Shrub	4.80	1.1136	14.20	6.6963	19.00	6.8920
AF	Deciduous forest	1.20	0.4899	9.00	4.0620	10.20	4.1881
	Field	1.00	0.0000	11.00	1.0000	12.00	1.0000
	Grain	3.80	0.8602	16.60	3.1241	20.40	3.6959
	Mixed forest	0.40	0.4000	2.60	1.4000	3.00	1.4142
	Potato	2.20	0.7348	20.00	4.6043	22.20	5.0339
	Riparian	2.20	0.6633	8.60	2.5020	10.80	2.8178
	Shrub	0.00	0.0000	9.20	1.8276	9.20	1.8276
RF	Apple	3.80	1.4967	11.80	0.9695	15.60	1.9131
	Field	11.80	2.5179	17.60	2.9428	29.40	2.2935
	Grain	31.80	7.6118	40.20	13.1583	72.00	20.7340
	Mixed forest	6.40	1.7205	9.00	3.9370	15.40	5.0060
	Mixed organic crops	27.80	5.4900	48.60	13.5300	76.40	16.7946
	Potato	22.60	4.4788	41.60	11.1203	64.20	15.3668
2005	Riparian	0.40	0.2449	4.60	1.7205	5.00	1.7607
FR	Mixed forest	1.60	0.6000	4.40	1.8601	6.00	2.1679
	Potato	2.80	0.9165	11.40	1.8055	14.20	1.9339
	Shrub	1.60	0.4000	6.60	2.4617	8.20	2.2226
LT	Coniferous forest	0.60	0.2449	0.40	0.2449	1.00	0.4472
	Deciduous forest	0.00	0.0000	0.20	0.2000	0.20	0.2000
	Field	4.20	0.8602	21.20	5.7393	25.40	5.5642
	Mixed forest	1.00	0.6324	0.20	0.2000	1.20	0.5831
	Riparian	1.20	0.2000	7.00	1.8974	8.20	1.8276
	Shrub	4.80	3.1528	11.60	3.1241	16.40	2.2935
AF	Deciduous forest	0.80	0.2000	16.40	5.1730	17.20	5.2288
	Field	3.20	0.9165	10.20	2.0833	13.40	2.2494
	Grain	4.20	0.7348	15.60	3.9699	19.80	4.5541
	Mixed forest	0.40	0.2449	0.60	0.6000	1.00	0.5477
	Potato	2.00	0.8367	18.60	2.8740	20.60	2.7857
	Riparian	3.60	1.1662	2.60	1.2083	6.20	1.9339
	Shrub	2.40	1.6613	33.40	15.7658	35.80	15.3375
PI	Field	1.00	0.3162	1.80	0.6633	2.80	0.7348
	Mixed forest	0.40	0.2449	1.40	0.6782	1.80	0.4899
RF	Apple	3.40	0.7483	5.20	1.4967	8.60	2.1354
	Grain	40.00	11.9541	48.80	7.9272	88.80	14.5959
	Mixed forest	1.80	0.5831	13.00	2.7019	14.80	2.3108
	Potato	27.20	7.0951	60.60	15.2302	87.80	21.3762
	Riparian	2.00	0.8944	9.20	2.6533	11.20	2.5377

[a] Location abbreviations: FR, commercial potato farm, Fryeburg, ME; LT, Orono Land Trust Land, Orono, ME; RF, University of Maine's Rogers Farm, Orono, ME; CR, commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, ME; PI, rural residential property, Presque Isle, ME; AF, University of Maine's Aroostook Research Farm, Presque Isle, ME.

uordecimguttata (L.), and *Anatis quindecimpunctata* (Olivier).

In both 2004 and 2005, *P. quatuordecimpuncata* was the most abundant species in field, potato, and mixed organic habitats; the mildew-feeding *P. vigintimaculata* in coniferous forest, deciduous forest, and mixed forest; and *H. axyridis* in apple. In grain, *P. quatuordecimpuncata* was the most abundant in Presque Isle, but *C. maculata* was the most abundant at the more southern, Orono location. Two habitats (riparian and shrub) differed in 2004–2005. In both of them, *P. vigintimaculata* was the most abundant in 2004, but *P. quatuordecimpuncata* was the most abundant in 2005.

When the data set was limited to aphidophagous species only, the totals became 2,338 in 2004 and 2,053 in 2005. In 2004, 66.19 ± 4.91% (mean ± SE) of all aphidophagous lady beetles captured by yellow sticky traps were non-native species. Similarly in 2005, 67.24 ± 4.26% were non-native. Among non-native aphidophagous species, *P. quatuordecimpuncata* was by far the most numerous lady beetle collected (54.75 and 57.67% of the total number of aphidophagous lady beetles collected in 2004 and 2005, respectively), followed by *H. axyridis* (6.97 and 11.98%) and *C. septempunctata* (4.28 and 3.07%). The two most abundant native aphidophagous lady beetles were *C. maculata*

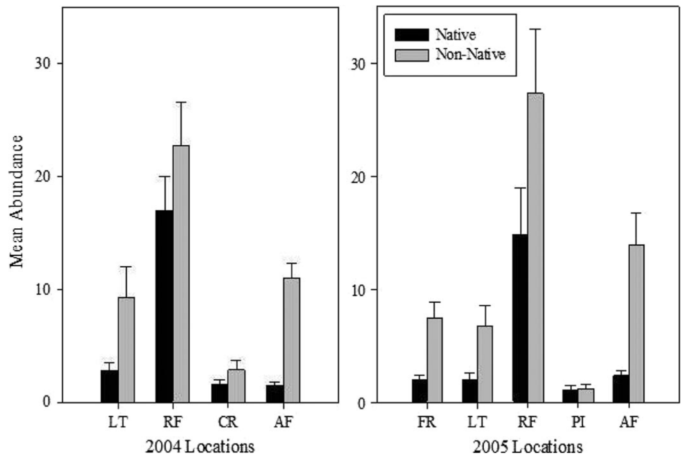

Fig. 1. Abundance per trap (all collection dates pooled) of non-native and native lady beetles at different locations.

(22.28% in 2004 and 14.95% in 2005) and *C. trifasciata* (3.21% in 2004 and 2.68% in 2005).

During both years of the study, there was considerable variation in the capture of aphidophagous lady beetles among sampled habitats at each location (Table 2). In 2004, mixed organic crops yielded the greatest number of lady beetles (native and non-native species combined), followed by grain and potato. Similarly, grain and potato yielded the highest numbers of beetles in 2005. In both 2004 and 2005, the fewest lady beetles were collected in coniferous forest, mixed forest, and deciduous forest. Statistically, the differences among the habitats were significant on the farm enrolled in the Conservation Reserve Program in Monticello in 2004 (df = 4, 40; $F = 2.89$; $P = 0.0342$; ANOVA) and on the commercial potato farm in Fryeburg in 2005 (df = 2, 24; $F = 3.82$; $P = 0.0363$; ANOVA). In all other cases, the difference was highly significant ($P < 0.0001$; ANOVA). The only exception was the rural residential property in Presque Isle sampled in 2005, where the difference between the two sampled habitats (field and mixed forest) was not significant (df = 1, 16; $F = 1.51$; $P = 0.2375$; ANOVA).

Non-native lady beetles were generally more abundant during both years at each location (Fig. 1; Table 3), with the exception of two locations where there was no difference (the farm enrolled in the Conservation Reserve Program in Monticello in 2004 and on the rural residential property in Presque Isle in 2005). There were significant interactions between lady beetle origin and the habitat where they were captured at Orono Land Trust both in 2004 (df = 5, 48; $F = 3.95$; $P = 0.0044$; ANOVA) and in 2005 (df = 5, 48; $F = 4.86$; $P = 0.0011$; ANOVA) and at the Aroostook Research Farm in 2005 (df = 6, 56; $F = 5.33$; $P = 0.0002$; ANOVA). Non-native lady beetles were more abundant in some of the habitats at these locations, and there was no significant difference between native and non-native species in the other habitats (Table 4). Never were the native species statistically more abundant than non-native species (Table 4). In the other locations sampled during the 2 yr of the study, non-native species were more abundant than native species regardless of habitat, as evidenced by statistically insignificant interaction terms ($P > 0.05$; ANOVA). There was a strong positive correlation between the abundance of non-native and native lady beetles (Fig. 2) in 2004 ($r = 0.7113$, $P < 0.0001$) and 2005 ($r = 0.5953$, $P < 0.0001$); where non-native abundance was high, so was native abundance.

Discussion

After their establishment in North America, non-native lady beetles now comprise a considerable proportion of the total lady beetle community in agricultural habitats (Wheeler and Hoebeke 1995, Elliott et al. 1996, Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002, Turnock et al. 2003, Brown 2003, Alyokhin and Sewell 2004). Our survey indicates that a similar situation exists in other types of habitats as well, at least in the examined areas of Maine. Despite considerable variation in the number of lady

Table 3. Results of ANOVA comparing mean number of native and non-native aphidophagous lady beetles captured at the surveyed Maine locations

Yr	Location[a]	df	*F*	*P*
2004	LT	1, 48	15.45	0.0003
2004	RF	1, 56	5.04	0.0287
2004	CR	1, 40	0.31	0.5820
2004	AF	1, 56	106.48	<0.0001
2005	FR	1, 24	14.98	0.0007
2005	LT	1, 48	16.00	0.0002
2005	RF	1, 40	15.01	0.0004
2005	PI	1, 16	0.12	0.7388
2005	AF	1, 56	45.44	<0.0001

[a] Location abbreviations: FR, commercial potato farm, Fryeburg, ME; LT, Orono Land Trust Land, Orono, ME; RF, University of Maine's Rogers Farm, Orono, ME; CR, commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, ME; PI, rural residential property, Presque Isle, ME; AF, University of Maine's Aroostook Research Farm, Presque Isle, ME.

Table 4. Mean number of native and non-native aphidophagous lady beetles captured in different habitats at locations where the interaction between beetle origin and habitat was significant

Location[a]	Habitat	Origin	Mean	SE	T^b	P^b
LT (2004)	Coniferous forest	Native	0.2000	0.2000	1.00	0.3739
		Non-native	0.0000	0.0000		
	Deciduous forest	Native	0.4000	0.2449	0.22	0.8362
		Non-native	0.6000	0.4000		
	Field	Native	11.0000	0.4472	8.01	0.0013
		Non-native	35.8000	3.3377		
	Mixed forest	Native	0.4000	0.4000	0.26	0.8099
		Non-native	0.4000	0.2449		
	Riparian	Native	0.4000	0.4000	6.70	0.0026
		Non-native	5.0000	2.5495		
	Shrub	Native	4.8000	1.1136	0.99	0.3770
		Non-native	14.2000	6.6963		
LT (2005)	Coniferous forest	Native	0.6000	0.2449	1.00	0.3739
		Non-native	0.4000	0.2449		
	Deciduous forest	Native	0.0000	0.0000	1.00	0.3739
		Non-native	0.2000	0.2000		
	Field	Native	4.2000	0.8602	3.67	0.0214
		Non-native	21.2000	5.7393		
	Mixed forest	Native	1.0000	0.6324	0.86	0.4388
		Non-native	0.2000	0.2000		
	Riparian	Native	1.2000	0.2000	3.95	0.0168
		Non-native	7.0000	1.8974		
	Shrub	Native	4.8000	3.1528	1.37	0.2417
		Non-native	11.6000	3.1241		
AF (2005)	Field	Native	3.2000	0.9165	3.24	0.0315
		Non-native	10.2000	2.0833		
	Deciduous forest	Native	0.8000	0.2000	4.40	0.0117
		Non-native	16.4000	5.1730		
	Grain	Native	4.2000	0.7348	3.30	0.0301
		Non-native	15.6000	3.9699		
	Mixed forest	Native	0.4000	0.2449	0.10	0.9273
		Non-native	0.6000	0.6000		
	Potato	Native	2.0000	0.8367	5.32	0.0060
		Non-native	18.6000	2.8740		
	Riparian	Native	3.6000	1.1662	1.01	0.3688
		Non-native	2.6000	1.2083		
	Shrub	Native	2.4000	1.6613	2.65	0.0571
		Non-native	33.4000	15.7658		

[a] Location abbreviations: LT, Orono Land Trust Land, Orono, ME; AF, University of Maine's Aroostook Research Farm, Presque Isle, ME.
[b] *t* and *P* values are for the follow-up paired *t*-tests.

beetles belonging to different species and collected in different habitats and locations, all surveyed communities of aphidophagous lady beetles had a large proportion of non-native species.

Based on the results of the correlation analyses, both native and non-native species seemed to prefer living in the same areas, suggesting that their abundances are strongly influenced by prey abundance (Kajita et al. 2000). This is likely to intensify competition for food and other resources, as well as intraguild predation. Competitive interactions between native and non-native species are asymmetric for some species, with the former at a competitive disadvantage compared with the latter (Michaud 2002, Yasuda et al. 2004). Therefore, competitive displacement of native lady beetles is a likely outcome of the establishment of non-native lady beetles in an area. Indeed, several studies that analyzed multiyear time series data on relative abundance of native and non-native lady beetles generally confirmed a decrease in the proportion of native beetles after the arrival of non-native species (Elliott et al. 1996, Brown and Miller 1998; Turnock et al. 2003; Evans 2000, 2004; Alyokhin and Sewell 2004).

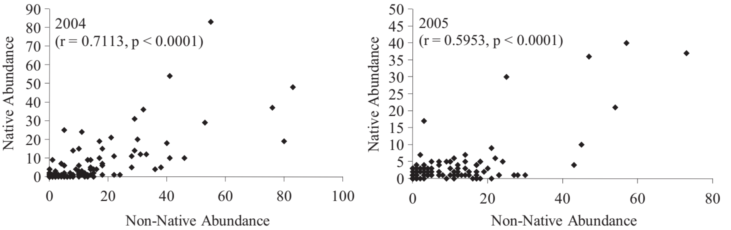

Fig. 2. Abundance per trap (all collection dates pooled) of non-native and native lady beetles in 2004 and 2005.

Lady beetle densities were generally lower in nonagricultural habitats surveyed compared with agricultural habitats (Table 2). Furthermore, there was some indication that their abundance in nonagricultural habitats was in some cases influenced by proximity to agricultural habitats. For example, lady beetle mean abundance (Table 2) in mixed forest was 0.80 (2004) and 1.2 (2005) at Orono Land Trust, where there was no agriculture, but 15.40 (2004) and 14.80 (2005) at Rogers Farm.

We found no evidence that native lady beetles have retreated to and remain dominant in nonagricultural habitats in response to the arrival of non-native lady beetles in agricultural habitats. Native lady beetle captures were never greater than non-native lady beetle captures in any habitat, regardless of the location or proximity to agriculture. This is inconsistent with findings by Evans (2000, 2004), who observed that although native lady beetles declined dramatically in Utah alfalfa fields after the establishment of *C. septempunctata,* they still dominated in the native habitats. For example, on native riparian vegetation and adjacent sagebrush, *C. septempunctata* accounted for only 3% of adult lady beetles (Evans 2000). It is possible that differences in landscape and habitat structure made nonagricultural habitats in Maine more prone to invasion than nonagricultural habitats in Utah. Alternatively, it is possible that *P. quatuordecimpuncata* and *H. axyridis,* which were the dominant species in our survey, but absent in the study by Evans (2000, 2004), are more invasive than *C. septempunctata.* Indeed, Brown and Miller (1998) and Alyokhin and Sewell (2004) reported replacement of *C. septempunctata* by the more recently arrived *H. axyridis.* Also, biological invasion is a dynamic and long-term process (Williamson 1996), so that non-native lady beetles in Utah might not have yet spread to more marginal habitats at the time of surveys (Evans 2000, 2004).

The considerable presence of non-native lady beetles in nonagricultural habitats may be of substantial conservation concern. Non-native lady beetles may replace native species, thus decreasing diversity and altering system dynamics. The replacement of native species with non-native species may alter predator–prey interactions, as non-native species may or may not exhibit the same prey preferences. Additionally, non-native lady beetles may prey on species of ecological concern. For example, *C. septempunctata* has been documented to consume larvae of the endangered Karner blue butterfly, *Lycaeides melissa samuelis* Nabokov (Schellhorn et al. 2005).

The exact ecological ramifications of the establishment of non-native lady beetles still remain to be determined. Many studies to date, including this study, focus primarily on comparisons of numbers. This provides valuable, but somewhat limited, information. For example, the ecological role of an individual *H. axyridis* may not equal that of an individual *H. convergens.* Therefore, comparisons of numbers alone are not sufficient in fully assessing the effects of non-native species introductions on native communities.

We found no evidence to support the "compression hypothesis" (MacArthur and Pianka 1966, MacArthur and Wilson 1967), which in this case, would have predicted that native lady beetles have retreated to and remain dominant in nonagricultural habitats in response to the arrival of non-native lady beetles in agricultural habitats. Our survey indicates that non-native lady beetles now comprise a considerable proportion of the total lady beetle community in both agricultural and nonagricultural habitats in the examined areas of Maine. Because naturally occurring, native lady beetles are an important component of biological control programs (Obrycki and Kring 1998), it is essential to understand their interactions with potential biological control organisms, native or non-native to the area of release.

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References Cited

Alyokhin, A., and G. Sewell. 2004. Changes in lady beetle community following the establishment of three alien species. Biol. Invasions 6: 463–471.

Bourque, D., D. S. Chandler, R. Dearborn, C. Donahue, and D. Michaud. 2005. An annotated list of Maine beetle families. Special Insert. Maine Entomol. 9(2).

Brown, M. W., and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis.* Entomol. News 109: 136–142.

Brown, M. W. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis.* Biocontrol 48: 141–153.

Chantal, C. 1972. Additions a la faune coleopterique du Quebec. Nat. Can. 99: 243–244.

Colunga-Garcia, M., and S. H. Gage. 1998. Arrival, establishment, and habitat use of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environ. Entomol. 27: 1574–1580.

Cormier, C. M., T. A. Forbes, T. A. Jones, R. D. Morrison, and D. B. McCorquodale. 2000. Alien invasion: the status of non-native lady beetles (Coleoptera: Coccinellidae) in industrial Cape Breton, Nova Scotia. Northeast Nat. 7: 241–247.

Day, W. H., D. R. Prokrym, D. R. Ellis, and R. J. Chianese. 1994. The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the

United States, and thoughts on the origin of this species and five other exotic lady beetles in Eastern North America. Entomol. News 105: 244–256.

Dixon, A.F.G. 2000. Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge University Press, Cambridge, United Kingdom.

Elliott, N., R. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia (Berl.) 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. Eur. J. Entomol. 97: 469–474.

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

Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. J. N.Y. Entomol. Soc. 93: 1–912.

Hodek, I. 1973. Biology of Coccinellidae. Dr. W. Junk N. V., Publishers, The Hague, The Netherlands.

Kajita, Y., F. Takano, H. Yasuda, and B. K. Agarwala. 2000. Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. Appl. Entomol. Zool. 35: 473–479.

Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis:* a review of its biology, uses in biological control, and non-target impacts. J. Insect Sci. 3:32. (http://www.insectscience.org/3.32/Koch_JIS_3_32_2003.pdf)

Koch, R. L., and T. L. Galvan. 2008. Bad side of a good beetle: the North American experience with *Harmonia axyridis*, pp. 23–35. *In* H. E. Roy and E. Wajnberg [eds.], From biological control to invasion: the ladybird *Harmonia axyridis* as a model species. Springer, Amsterdam, The Netherlands.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. 100: 603–609.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Mensah, R. K. 1997. Yellow traps can be used to monitor populations of *Coccinella transversalis* (F.) and *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) in cotton crops. Aust. J. Entomol. 36: 377–381.

Michaud, J. P. 2002. Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea.* Environ. Entomol. 31: 827–835.

Obrycki, J. J., and T. J. Kring. 1998. Predaceous Coccinellidae in biological control. Annu. Rev. Entomol. 43: 295–321.

Parajulee, M. N., and J. E. Slosser. 2003. Potential of yellow sticky traps for lady beetle survey in cotton. J. Econ. Entomol. 96: 239–245.

SAS Institute. 2002. PROC user's manual, version 9th ed. SAS Institute, Cary, NC.

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

Schellhorn, N. A., C. P. Lane, and D. M. Olson. 2005. The co-occurrence of an introduced biological control agent (Coleoptera: *Coccinella septempunctata*) and an endangered butterfly (Lepidoptera: *Lycaeides melissa samuelis*). J. Insect Conserv. 9: 41–47.

Stephens, E. J., and J. E. Losey. 2004. Comparison of sticky cards, visual and sweep sampling of coccinellid populations in alfalfa. Environ. Entomol. 33: 535–539.

Turnock, W. J., I. L. Wise, and F. O. Matheson. 2003. Abundance of some native coccinellids (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata.* Can. Entomol. 135: 391–404.

Wheeler, A. G., and E. R. Hoebeke. 1995. *Coccinella novemnotata* in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proc. Entomol. Soc. Wash. 97: 701–716.

Williamson, M. 1996. Biological invasions. Chapman & Hall, London, England.

Yasuda, H., E. W. Evans, Y. Kajita, K. Urakawa, and T. Takizawa. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. Oecologia (Berl.) 141: 1432–1939.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.

Zaviezo, T., A. A. Grez, C. F. Estades, and A. Perez. 2006. Effects of habitat loss, habitat fragmentation, and isolation on the density, species richness, and distribution of ladybeetles in manipulated alfalfa landscapes. Ecol. Entomol. 31: 646–656.

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Appendix 1. Mean numbers ($N = 5$) of lady beetle species captured on yellow sticky cards throughout the sampling season in each habitat by location

2004 CR[a]	Coniferous forest		Field		Mixed forest		Riparian		Shrub	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native species										
Coccinella hieroglyphica									0.20	0.2000
Coccinella septempunctata							0.20	0.2000		
Harmonia axyridis							0.40	0.4000		
Propylea quatuordecimpunctata			2.40	1.9391	3.60	1.3266	6.20	2.8879	3.20	0.7348
Native species										
Chilocorus sp.					0.40	0.2449			0.20	0.2000
Coccinella trifasciata			0.20	0.2000	0.20	0.2000				
Coleomegilla maculata			0.80	0.8000						
Hippodamia parenthesis			0.20	0.2000					0.20	0.2000
Hyperaspis sp.			0.40	0.2449						
Mulsantina sp.	1.20	0.8000					0.20	0.2000		
Psyllobora vigintimaculata	1.60	0.6000	0.20	0.2000	3.20	1.2410	13.20	7.7614	10.00	5.8822
Scymnus sp.			0.80	0.5831			0.20	0.2000		

2004 LT[a]	Coniferous forest		Deciduous forest		Field		Mixed forest		Riparian		Shrub	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native species												
Coccinella septempunctata					1.80	0.3742						
Harmonia axyridis					4.20	1.2410			0.20	0.2000		
Propylea quatuordecimpunctata			0.60	0.4000	29.80	3.6387	0.40	0.2449	4.80	2.6344	19.20	5.8600
Native species												
Chilocorus sp.	0.20	0.2000			0.20	0.2000						
Coccinella transversoguttata					0.20	0.2000						
Coccinella trifasciata					6.40	1.2083					0.80	0.4899
Coleomegilla maculata					0.40	0.4000						
Hippodamia parenthesis					0.80	0.3742						
Psyllobora vigintimaculata	3.00	1.8974	6.20	3.8262	0.60	0.4000	2.40	0.8124	28.00	10.7098	4.40	1.5033
Scymnus sp.					0.40	0.2450	0.40	0.2450	0.20	0.2000		

2004 AF[a]	Deciduous forest		Field		Grain		Mixed forest		Potato		Riparian		Shrub	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native species														
Coccinella hieroglyphica			0.20	0.2000										
Coccinella septempunctata			1.40	0.5099	1.60	0.5099			2.00	0.8367				
Harmonia axyridis	0.20	0.2000	0.20	0.2000					1.40	0.9274			0.20	0.2000
Propylea quatuordecimpunctata	8.60	4.2497	7.40	1.8601	14.80	2.9732	2.60	1.4000	16.60	5.1245	10.00	3.0332	9.00	1.6733
Native species														
Adalia bipunctata											0.20	0.2000		
Anatis quindecimpunctata	0.20	0.2000												
Anisoticta bitriangularis											0.60	0.4000		
Calvia quatourdecimguttata			0.20	0.2000										
Chilocorus sp.	0.20	0.2000												
Coccinella trifasciata	0.60	0.6000	2.40	1.6912	0.60	0.4000			0.20	0.2000				
Coleomegilla maculata					1.40	0.5099	0.40	0.4000	0.80	0.5831	0.40	0.4000		
Hippodamia parenthesis			0.40	0.2449	1.60	0.5099			0.20	0.2000	0.40	0.4000		
Psyllobora vigintimaculata	24.80	9.5205					49.20	24.5039	0.40	0.2449	9.80	7.3716	39.00	20.3666

2004 RF[a]	Apple		Field		Grain		Mixed organic		Mixed forest		Potato		Riparian	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native species														
Coccinella septempunctata			4.40	0.5099	2.40	0.4000	1.00	0.3162	0.20	0.2000	5.00	1.1402		
Epilachna varivestis							0.80	0.8000	0.40	0.4000				
Harmonia axyridis	11.00	0.8944	0.60	0.4000	2.20	0.4899	7.20	2.2226	0.60	0.4000	4.00	1.4832	0.20	0.2000
Propylea quatuordecimpunctata	0.80	0.3742	6.20	2.8531	27.20	7.0810	40.20	13.2151	8.20	3.4843	32.00	9.7417	4.40	1.5684
Native species														
Chilocorus sp.							0.20	0.2000						
Coccinella trifasciata			0.20	0.2000	1.20	0.2000	1.00	0.5477			1.20	0.5831		
Coccinella transversoguttata					0.20	0.2000								
Coleomegilla maculata	3.80	1.4967	13.00	3.1623	35.60	11.6645	25.60	5.0458	4.40	1.6310	17.20	2.6344	0.40	0.2449
Hippodamia parenthesis			2.60	0.5099	0.80	0.4899	0.60	0.4000			3.60	1.2884		
Hippodamia variegata			0.20	0.2000			0.20	0.2000			0.60	0.2449		
Psyllobora vigintimaculata	0.80	0.4899			6.60	1.1662	0.60	0.4000	17.40	5.9211	3.20	2.9563	7.40	4.1061
Scymnus sp.	0.80	0.3742												

2005 FR[a]	Mixed forest		Potato		Shrub	
	Mean	SE	Mean	SE	Mean	SE
Non-native species						
Coccinella septempunctata			4.20	1.5620		
Harmonia axyridis	1.80	1.1136	7.00	1.3038	5.40	1.8055
Propylea quatuordecimpunctata	2.60	1.0770	0.20	0.2000	1.20	0.8000
Native species						
Chilocorus sp.	0.40	0.2449				
Coccinella trifasciata					0.20	0.2000
Coleomegilla maculata	0.20	0.2000	1.40	0.5099	0.20	0.2000
Hippodamia parenthesis			1.00	0.5477		
Psyllobora vigintimaculata	52.00	27.4062			2.80	1.1136
Scymnus sp.	0.20	0.2000			0.40	0.2450

Continued on following page

Appendix 1. Continued

	Coniferous forest		Field		Mixed forest		Riparian		Shrub					
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE				
2005	Coniferous forest		Deciduous forest		Field		Mixed forest		Riparian		Shrub			
LT[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Non-native species														
Coccinella septempunctata					0.20	0.2000								
Harmonia axyridis	0.40	0.2449			0.60	0.2449			0.40	0.2449	1.00	0.6325		
Propylea quatuordecimpunctata			0.20	0.2000	20.40	5.6798	0.20	0.2000	6.60	1.9391	10.60	3.2031		
Native species														
Chilocorus sp.	0.40	0.2449					0.20	0.2000			0.20	0.2000		
Coccinella trifasciata					2.00	0.5477					0.20	0.2000		
Coleomegilla maculata					0.40	0.2449								
Hyperaspis sp.					0.20	0.2000			0.40	0.2449	1.00	0.6325		
Mulsantina sp.											3.20	3.2000		
Psyllobora vigintimaculata	1.60	0.6782	4.20	1.1136	0.60	0.4000	3.20	1.8276	4.40	0.8718	3.60	1.3638		
Scymnus sp.					1.00	0.5477			0.40	0.2450	0.60	0.4000		
2005	Deciduous forest		Field		Grain		Mixed forest		Potato		Riparian		Shrub	
AF[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Non-native species														
Coccinella hieroglyphica			0.60	0.4000									0.20	0.2000
Coccinella septempunctata			0.60	0.4000	0.20	0.2000			3.20	0.7348			0.20	0.2000
Harmonia axyridis	1.60	0.8124	0.60	0.4000					4.00	0.8367			0.60	0.4000
Propylea quatuordecimpunctata	14.80	5.1127	8.40	1.6912	15.40	3.8678	0.60	0.6000	11.40	2.7129	2.60	1.2083	32.40	15.9455
Native species														
Adalia bipunctata	0.20	0.2000	0.60	0.2449	0.20	0.2000							0.80	0.8000
Coccinella transversoguttata									0.20	0.2000				
Coccinella trifasciata	0.20	0.2000	1.00	0.3162	0.40	0.2449			1.00	0.6325	0.20	0.2000	0.80	0.5831
Coleomegilla maculata	0.20	0.2000												
Hippodamia convergens			0.20	0.2000										
Hippodamia parenthesis			0.20	0.2000					0.20	0.2000				
Hippodamia tredecimpunctata			0.40	0.2449	3.00	0.8367			0.40	0.2449	0.40	0.2449		
Hyperaspis sp.			0.40	0.2449										
Mulsantina sp.											0.80	0.3742		
Psyllobora vigintimaculata	12.80	3.7202	1.00	1.0000	2.20	1.1136	41.60	30.0576	0.20	0.2000	4.60	2.7677	23.80	10.9563
Scymnus sp.			0.20	0.2000							0.60	0.4000	0.40	0.4000
2005	Field		Mixed forest											
PI[a]	Mean	SE	Mean	SE										
Non-native species														
Coccinella septempunctata	0.20	0.2000	0.20	0.2000										
Harmonia axyridis	0.20	0.2000												
Propylea quatuordecimpunctata	1.40	0.5099	0.20	0.2000										
Native species														
Coccinella trifasciata	0.20	0.2000												
Psyllobora vigintimaculata	1.40	1.4000	8.40	3.0100										
2005	Apple		Grain		Mixed forest		Potato		Riparian					
RF[a]	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE				
Non-native species														
Coccinella septempunctata	0.20	0.2000	1.20	0.5831			2.20	0.9695						
Harmonia axyridis	3.20	1.0198	7.60	1.8601	0.60	0.2449	13.00	5.5136	1.20	0.8000				
Propylea quatuordecimpunctata	1.80	0.3742	40.00	8.6197	12.40	2.7677	45.40	10.7219	8.00	2.2361				
Native species														
Adalia bipunctata					0.20	0.2000								
Chilocorus sp.	0.20	0.2000	0.20	0.2000	0.20	0.2000			0.20	0.2000				
Coccinella trifasciata	0.60	0.4000	1.00	0.5477			3.20	1.4629						
Coleomegilla maculata	0.60	0.4000	36.20	12.8039	0.20	0.2000	21.80	6.3356	0.20	0.2000				
Hippodamia convergens			1.60	1.6000										
Hippodamia parenthesis			0.60	0.4000			1.20	0.3742						
Hippodamia tredecimpunctata			0.20	0.2000			0.60	0.4000						
Hyperaspis sp.	0.40	0.2449			0.40	0.2449	0.20	0.2000	0.20	0.2000				
Psyllobora vigintimaculata	1.80	0.5831	0.60	0.2449	23.60	9.1630	0.20	0.2000	4.00	2.2583				
Scymnus sp.	0.80	0.4472							0.60	0.2450				

[a] Location abbreviations: FR, commercial potato farm, Fryeburg, ME; LT, Orono Land Trust Land, Orono, ME; RF, University of Maine's Rogers Farm, Orono, ME; CR, commercial potato farm currently enrolled in the Conservation Reserve Program, Monticello, ME; PI, rural residential property, Presque Isle, ME; AF, University of Maine's Aroostook Research Farm, Presque Isle, ME.