

Review

Interactions Among Native and Non-Native Predatory Coccinellidae Influence Biological Control and Biodiversity

Hongran Li,^{1,2} Baoping Li,² Gábor L. Lövei,³ Timothy J. Kring,⁴ and John J. Obrycki^{1,5}

¹Department of Entomology, University of Kentucky, Lexington, KY 40546, USA, ²Department of Entomology, School of Plant Protection, Nanjing Agricultural University, Nanjing, Jiangsu Province 210095, China, ³Department of Agroecology, Aarhus University, Flakkebjerg Research Centre, Forsøgsvej 1, DK-4200 Slagelse, Denmark, ⁴Department of Entomology, Virginia Tech, Blacksburg, VA 24061, USA, and ⁵Corresponding author, e-mail: john. obrycki@uky.edu

Subject Editor: Gadi VP Reddy

Received 30 September 2020; Editorial decision 31 October 2020

Abstract

Over the past 30 yr, multiple species of predatory Coccinellidae, prominently *Coccinella septempunctata* L. and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) have spread to new continents, influencing biodiversity and biological control. Here we review the mechanisms underlying these ecological interactions, focusing on multi-year field studies of native and non-native coccinellids and those using molecular and quantitative ecological methods. Field data from Asia show that *H. axyridis*, *C. septempunctata*, and *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae) are regularly among the most abundant predatory species but their rank varies by habitat. Studies of these species in their native Asian range, primarily related to their range in mainland China, document different patterns of seasonal abundance, species specific associations with prey, and habitat separation. Intraguild predation is well documented both in Asia and in newly invaded areas, and *H. axyridis* benefits most from this interaction. *Harmonia axyridis* also seems to rely more on cannibalism in times of prey scarcity than other species, and relatively sparse data indicate a lower predation pressure on it from natural enemies of coccinellids. Declines in the abundance of native coccinellids following the spread and increase of non-native species, documented in several multi-year studies on several continents, is a major concern for native biodiversity and the persistence of native coccinellid species. We suggest that future studies focus more attention on the community ecology of these invasive species in their native habitats.

Key words: biological control, biodiversity, ecological interactions, invasive species

Introduction

Coccinellids have long been considered important biological control organisms (Obrycki and Kring 1998), but current interest in predatory coccinellid beetles continues to grow. Various aspects have been reviewed, including trophic ecology (Lundgren and Webber 2009), invasion ecology (Roy and Wajnberg 2008, Brown et al. 2017), and several syntheses of the role of coccinellids in biological control (Powell and Pell 2007, Volkl et al. 2007, Michaud and Harwood 2012, Michaud 2012). During the past three decades, several species of predatory Coccinellidae have spread to new continents (Franzmann 2002, Rebolledo et al. 2009, Lombaert et al. 2010, Evans et al. 2011, Soares et al. 2018), prominently *Coccinella septempunctata* L. and *Harmonia axyridis* (Pallas), causing significant ecological effects in their new environments (Obrycki et al. 2000, Roy et al. 2016, Camacho-Cervantes et al. 2017, Rondoni et al. 2020). Both species are now distributed widely on most

continents (Poutsma et al. 2008, Brown et al. 2011, Evans et al. 2011, Kajita et al. 2012, Mukwevho et al. 2017, CABI Invasive Species Compendium (<https://www.cabi.org/isc/datasheet/26515>) (<https://www.cabi.org/isc/datasheet/11733>). Several papers have discussed the positive and negative effects of *C. septempunctata* and *H. axyridis* in new environments (e.g., Harmon et al. 2007, Lucas et al. 2007, Koch and Galvan 2008, Camacho-Cervantes et al. 2017, Kenis et al. 2017, Koch and Costamagna 2017, Riddick 2017). The interactions of these two predatory species with native lady beetle species influences community structures and predator–prey dynamics in a wide range of ecosystems, including agroecosystems. Thus, the range expansion of these predatory species has both negative and positive ecological effects on biodiversity and levels of biological control. In this review, we examine whether these interactions vary between the native and non-native ranges for specific species (e.g., *H. axyridis* and *C. septempunctata*).

Discussion of interactions among predatory species should consider recent documented declines in the abundance and biomass of several arthropod taxa (Sanchez-Bayo and Wyckhuys 2019, Bell et al. 2020, Didham et al. 2020, van Klink et al. 2020, Wagner 2020). The species discussed in this review are typically studied within a guild of predatory species interacting with their (mostly) aphid prey (Obrycki et al. 2009; Kindlmann et al. 2010, 2011), although many coccinellids also feed on other arthropods, fungi, and plant materials (e.g., nectar and pollen) (Evans 2009, Lundgren and Weber 2009, Hodek and Evans 2012, Ugine et al. 2019). Short- and long-term changes in the abundance of prey species are likely to affect the abundance of native and non-native predatory species due to reductions in resources, which influence their interactions via increased competition.

In a recent review of the role of non-native lady beetles in the biological control of insect pests, Rondoni et al. (2020) presented case studies of *C. septempunctata* and *H. axyridis* in North America, *H. axyridis* in Europe, and *H. axyridis* and *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) in South America. In this review, we complement Rondoni et al. (2020), by 1) emphasizing the interactions among *H. axyridis* and *C. septempunctata* and other lady beetles in their native ranges in Asia, including the Chinese literature, and 2) providing a broader ecological analysis of the effects of non-native coccinellids in their new environments.

Criteria for Selecting and Evaluating the Literature

We primarily considered the literature from 1997 to 2020 on the interactions between native and non-native predatory Coccinellidae, to highlight what we have learned about mechanisms underlying these ecological interactions. Our focus is on multi-year (≥ 3 yr) field studies, that provide quantitative data related to biodiversity and/or biological control and field studies quantifying the interactions among native and non-native species. Several studies have examined interactions between non-native coccinellids and other taxa in the aphid predator guild (e.g., Royer et al. 2008, Meisner et al. 2011, Howe et al. 2016, Wells et al. 2017) but our review is restricted to interactions between native and non-native Coccinellidae. Laboratory-based or greenhouse studies were considered only if tied directly to field studies. Numerous studies and reviews (e.g., Lucas 2005, 2012; Moser and Obrycki 2009; Katsanis et al. 2013; Gkounti et al. 2014; Mirande et al. 2015), that documented intraguild predation (IGP) among native and non-native species under laboratory conditions were not included, unless they provided insights into mechanisms underlying field interactions.

The second section of this review examines the literature related to coccinellid community ecology and interactions in their native Asian ranges. In contrast to the previous section, in which *H. axyridis* and *C. septempunctata* are non-native species, in this section they are native species within their home ranges. We also summarize cases of introduced non-native coccinellids in Asia (Table 1), which are fewer than the 26 non-native species established in North America (Gordon 1985). Interactions within the native range are considered based on mechanisms for species coexistence proposed by Chesson (2000): resource partitioning, frequency dependent mortality by natural enemies (of Coccinellidae), and fluctuations in populations and environmental factors. Knowledge about the interactions of these lady beetles in their native range may expand our understanding of the mechanisms behind their successful invasion.

Finally, we address the need for comparative studies of Coccinellidae in their native and non-native ranges to quantify intra-specific differences in these species. We also discuss experimental

Table 1. Asian introductions of Coccinellidae

Species	Location/country	Date	Intentional introduction	Target insect	Habitat in new range	Distribution	Reference
<i>Rodalia cardinalis</i>	Taiwan, Guangdong/China	1909	Yes	Cottony-cushion scale	Citrus orchards	Regional	Gu et al. 2000
<i>R. cardinalis</i>	Japan	1911	Yes	Cottony-cushion scale	Citrus orchards	Regional	Toda and Sakuratani 2006
<i>Cryptolaemus montrouzieri</i>	Guangdong and Fujian/China	1955	Yes	Mealybugs	Citrus orchards	Regional	Li 1993
<i>Olla v-nigrum</i>	Okinawa/Japan	1989	No	N/A	Green hedge and grasses	Local	Toda and Sakuratani 2006
<i>Adalia bipunctata</i>	Kobe/Japan	1993	No	N/A	Grasses & trees	Local	Sakuratani 1994, Toda and Sakuratani 2006
<i>Delphastus catalinae</i>	Fujian/China	1996	Yes	Whiteflies	Greenhouses	Local	Huang et al. 1998

approaches that may provide a fundamental understanding of the mechanisms underlying these interactions by combining ecological, molecular, and genetic techniques.

Interactions Between Native and Non-Native Predatory Coccinellidae

The successful establishment of several non-native coccinellids prompted extensive research exploring their interactions with extant native coccinellids sharing the same habitats (e.g., Elliott et al. 1996; Evans et al. 2011; Kindlmann et al. 2011; Bahlai et al. 2013, 2015; Grez et al. 2016; Honek et al. 2016; Brown and Roy 2018). The impact of non-native species on native intraguild predators was the focus of a majority of these studies, while fewer studies evaluated the impact on target prey (e.g., Alyokhin and Sewell 2004, Brown 2004, Koch and Costamagna 2017). Field studies commonly track the relative abundance of native and non-native coccinellid species and discuss the potential displacement of native species (Table 2) (e.g., Turnock et al. 2003, Alyokhin and Sewell 2004, Evans 2004, Brown and Roy 2018). Numerous controlled experiments in the laboratory have documented IGP with preferences for immobile stages, with examples of symmetric and asymmetric interactions among native and non-native species (Lucas 2005, 2012; Pell et al. 2008; Ware and Majerus 2008; de Castro-Guedes et al. 2020; Rasekh and Osawa 2020). IGP results in not only an energy gain by the IGP predator, but simultaneously reduces competition for resources among the predatory species and thus can trigger complex population dynamics (Polis et al. 1989, Fonseca et al. 2017). The net impact of IGP may be positive, negative, or neutral on the population dynamics of the common prey species as well as on the participating predator species (Polis et al. 1989).

Types of Interactions

The arrival of non-native predator species into an ecosystem may have complex and wide ranging effects on the dynamics of extant prey and predator species. Competitive exclusion of a resident predator by a non-native one may result in little or no impact on their common prey species even in a relatively simple food web (Snyder and Tylianakis 2012). Numerous multi-year field studies of recent coccinellid introductions have focused on the interactions among non-native and native species and changes in relative abundance of native ones (Table 2). These interactions among predators may be broadly classified as direct (e.g., IGP or interference competition) or indirect (e.g., competition for resources: exploitative or apparent).

Examining interactions between native and non-native predatory species of Coccinellidae to determine potential effects on the diversity of predatory guilds and levels of biological control requires multi-year studies using appropriate sampling methods for predator and prey (Honek et al. 2017) (Table 2). These long-term field studies may be combined with manipulative field studies, realistic greenhouse/field cage studies, and/or molecular gut analysis to provide a fundamental understanding of the population fluctuations of these interactions (e.g., Thomas et al. 2013, Brown and Roy 2018).

Several hypotheses have been proposed to describe the interactions between native and non-native Coccinellidae (Bahlai et al. 2015): 1) a non-native coccinellid exploits an ecological opportunity not utilized by native species, 2) IGP in which non-native predator species prey on native members of the guild, 3) exploitative competition where the non-native species displaces native ones because its life history characteristics (tolerance limits) allow it to outcompete

the natives (Snyder 2009, Hentley et al. 2016), and 4) habitat compression where native species are out-competed in some of their previous habitats and recede to their core habitats (Evans 2004).

The invasion history and life history characteristics of *H. axyridis* and *C. septempunctata* provide examples for three of the four hypotheses describing the potential interactions between native and non-native Coccinellidae (Hodek and Michaud 2008; Kajita and Evans 2010a, b; Hautier et al. 2017; Raak-van den Berg et al. 2017; Rondoni et al. 2017; Honek et al. 2020a).

1) An Unused Ecological Opportunity

We did not find literature supporting the hypothesis that non-native species use resources previously not used by native ones to explain their interactions with native coccinellids. This hypothesis has not been examined extensively, probably due to the observed declines in populations of native species corresponding with the presence in similar habitats and increases in populations of non-native species (Bahlai et al. 2015).

2) Intraguild Predation

Using a variety of techniques, numerous studies have documented IGP among native and non-native Coccinellidae in the field, frequently—but not always—favoring *H. axyridis* (see review by Pell et al. 2008, Hautier et al. 2011, Rank-van den Berg et al. 2012, de Castro-Guedes et al. 2020) (Table 3). However, the importance of IGP has been questioned (Kindlmann and Houdkova 2006, Hemptinne et al. 2012) and its importance may vary among regions and habitats. For example, in a caged tree study with sufficient aphid prey, *H. axyridis* IGP did not cause significant mortality of the native *Adalia bipunctata* (Raak-van den Berg et al. 2018). In North America, 61% of egg masses of native coccinellids were attacked in Michigan soybean fields, in which non-native *H. axyridis* and *C. septempunctata* were the most abundant predators and were assumed to be major intraguild predators (Gardiner et al. 2011). This field study indicated that IGP (both by native and non-native predators) contributed to the decline of native coccinellids. However, Smith and Gardiner (2013) reported that eggs of native coccinellids were consumed by a number of generalist species (e.g., Opiliones (harvestmen) and Stylommatophora (slugs)) at higher rates than those of *H. axyridis*. These results do not support the IGP by *H. axyridis* hypothesis as a mechanism explaining the decline of native coccinellids in North America (Smith and Gardiner 2013).

IGP may be an important outcome among and within generalist predators when common prey become scarce, allowing the survival of the immature population to develop to adults, reproduce, and/or disperse (Rondoni et al. 2018). In the context of interactions of native and non-native coccinellids, research has documented the negative aspects of IGP on native species (Rondoni et al. 2015, Brown and Roy 2018). However, Hemptinne et al. (2012) concluded that interspecific predation within aphidophagous guilds occurs in the field, but typically after declines in aphid infestations. In laboratory experiments, the presence of aphid prey reduces interspecific predation (Lucas 2005, 2012; Mirande et al. 2015); field experiments indicate that interspecific predation occurs within these guilds, but Hemptinne et al. (2012) propose that this interaction does not match the theoretical concept of IGP developed by Polis et al. (1989). Hemptinne et al. (2012) argue that the relatively rare occurrence of IGP in aphidophagous guilds is to be expected given that IGP implies top-down regulation of the extraguild prey, and given the ephemeral nature of aphid infestations, such control rarely occurs in these predator–aphid prey systems. Similarly, based on modeling and

Table 2. Studies of long-term trends in predatory Coccinellidae

Goals/hypothesis/objectives	Study period	Location	Habitat, sampling methods, and life stages collected	Results and conclusions	Reference
Europe					
Quantify changes in coccinellid community in lime and pine trees, and stinging nettles following <i>Ha</i> arrival	2006–2016	East Anglia, United Kingdom	Timed samples; beat sheets for trees and sweep nets for nettles; 1–2 samples/mo; Adults, L3, L4 counted	Significant negative relationship between <i>Ha</i> and A2 adults on lime trees. Change in coccinellid community structure. Strong indication that declines in A2 caused by <i>Ha</i> . Proportion of native spp. declined from 99.8 to 31%.	Brown and Roy 2018
Assess native species abundance and community composition on deciduous trees before and after <i>Ha</i> arrival	1976–1986, 2002–2006 vs. 2011–2014	Czech Republic	Before, just before, and after <i>Ha</i> arrival; May–July sweep net samples of adults; deciduous trees; 1–2 samples/mo	Collected 21 native and 1 non-native spp.; A2, C5, and P14 decreased; declines prior to <i>Ha</i> arrival; A10, Ca14 increasing prior to <i>Ha</i> but then declined. Shannon diversity for native species similar over 40 yr; Several factors (<i>Ha</i> , climate change, land use patterns) influence native species composition and long-term population fluctuations	Honek et al. 2016
Hypothesis: Long-term reductions in native species abundance correlated with high abundance and wide distribution of <i>Ha</i>	1976–1986 vs. 2010–2016	Czech Republic	Cereals, herbaceous habitats and trees; fortnightly sweep net samples of adults, L3, L4. Trees sampled Apr–Nov; cereals and herbaceous plants >30 cm until senescence	<i>Ha</i> adults and larvae most abundant species in trees; less abundant in cereals and herbaceous habitats. Relative abundance of native species declined by 50–70%	Honek et al. 2019
Document seasonal variation in species abundance and community composition on trees	2010–2014	Central Europe	Sweep net samples of adults every 2 wks; April to Nov.	Documented 21 spp.; seasonal trends similar over 5 yr; A10 most abundant sp. in May–June; <i>Ha</i> most abundant in late summer; Shannon diversity decreased during summer	Honek et al. 2015
Assess effects of land use changes and 1976–1983 vs. <i>Ha</i> on coccinellid communities	2002–2010	Central Europe	One sample/year, Jun/Jul., Cereal crops, wild herbaceous plants, deciduous trees. 1976–1983: intensive agriculture: high pesticide & fertilizer use, higher crop diversity; 2002–2010: decrease in arable land, fertilizer/pesticide use; increased monoculture; presence of <i>Ha</i>	Similar mean no. spp. on trees (3.18) and herbaceous habitats (3.06); cereals: 2.63 spp.; similar community composition over 35 yr; Shannon diversity higher in 2002–2010.	Honek et al. 2014
1) evaluate <i>Ha</i> impact on lady beetle communities; 2) describe changes over 20 yr in community structure; 3) document native species decline after <i>Ha</i> arrival	1995–1996 vs. 2015–2016	N Italy	Before vs. after <i>Ha</i> arrival; adults sampled by beating from hedgerows and sweep-netting in herbaceous habitats at 6 sites; Apr–Oct. fortnightly (1995–1996), or monthly (2015–2016)	In 2015–2016, <i>Ha</i> at all 6 sites; most abundant species on trees and shrubs at five sites; decline in A2. Changes in natives species in shrubs/trees; native spp. 33% of all adults by 2015–2016. Low relative abundance of <i>Ha</i> in herbaceous habitats -little effect on native spp.	Maseri et al. 2018
North America					
Document effects of C7 on common native coccinellid species	1983–2001 & 1989–2001, 1989–2001	Manitoba, Canada	D-Vac & sweep net samples in alfalfa, sweep net and visual sampling in field crops and other vegetation; transect sampling of adult aggregations; spring & autumn	The relative abundance of native C tra, H con, H paren, C3 decreased after C7 establishment, due to competitive displacement by C7. By 1992, C7 dominant; Displacement of several natives might be a contributing factor in the slight increase in H13 because C7 may compete less directly with this native species	Turnock et al. 2003
Quantify changes in coccinellid community in potato plots before, during and after establishment of non-native species. Quantify changes in aphid densities infesting potatoes	1971–2001	Maine, USA	Weekly visual counts of lady beetle adults and aphids on 2.5 plants in potato plots	Density of lady beetle populations and relative abundance of individual lady beetle species varied yearly; before 1980 native C.tra & H13 very abundant; C7 6% in 1980, 100% in 1994; C. tra and H13 declined but persisted; P14 arrives in 1993, <i>Ha</i> in 1995; aphid densities reduced following arrivals	Alyokhin and Sewell 2004
Describe the native and non-native lady beetles in alfalfa fields in New Jersey and Delaware	1993–2004 & 1999–2004	New Jersey, Delaware, USA	Weekly (May–Jul.) or fortnightly (Aug.–Oct.) sweep net samples;	5 spp. abundant in alfalfa (2 native, 3 non-native; Four non-native species collected; Similarities in the five most abundant species at the two locations (separated by 161 km); native Co. mac most abundant at both locations; Comparisons of NJ data 5 yr before and after the occurrence of 3 non-native species—increase in number of native species, primarily Co. mac. Mentions reduction in pea aphid densities, but data not collected	Day and Tatum 2006

Table 2. Continued

Goals/hypothesis/objectives	Study period	Location	Habitat, sampling methods, and life stages collected	Results and conclusions	Reference
Quantify populations of C9 after C7 establishment in N American intermountain western region	1988–2015	Utah, USA	Samples (1–2/mo) taken May–Sept.; sweep net and visual samples	Low but persistent populations of C9 observed in alfalfa and native habitats as C7 increased in relative abundance; Size of adult C9 remains similar; no increase in larval competition for food due to C7.	Evans 2017
Test habitat compression hypothesis in which native species are restricted to certain habitats by the presence of non-native spp.	1992–2001	Utah, USA	Sweep net sampling of adults	C7 established and increased in numbers, densities of native species decreased; Decline in numbers of native spp. in alfalfa related to decrease in densities of pea aphids caused by C7.	Evans 2004
Hypothesis: Presence of C7 larvae will increase larval competition for food resulting in smaller adults of native species in alfalfa	1991–1997	Utah, USA	Sweep net sampling and/or hand collections of adults in alfalfa; multiple fields sampled except in 1 yr; generally weekly samples from late April to early June	Native species (C tra, H co, H5, H. sin, H13) declined as C7 increased. No reduction in adult size of native species; no evidence that C7 increased scramble competition for food among larvae; wide variation in C7 adult body size	Evans 2000
Describe lady beetle communities in apple orchards before/after Ha and C7 arrival and impact on spirea aphid	5 nonconsecutive years	W Virginia, USA	Visual observations of small trees—6 times/year; Weekly counts on branch terminals on larger trees; Counts on branch terminals 3–6 times/year	Individual species affected, but overall effect of Ha on predator guild negligible; Reduction in relative abundance of C7 by Ha; native coccinellids more abundant when only C7 present	Brown 2003
Document (1) population trends of 11 species of native coccinellids before/after Ha arrival (2) describe Ha population trends and habitat preferences	1989–1994 vs. 1994–1998	Michigan, USA	Before vs. after Ha arrival; 7 habitats; adults captured on yellow sticky cards changed fortnightly, May–Aug.	Variation in trends of native pp. after Ha: 3 spp. declined, 1 sp. declining prior to Ha, continued to decline, 3 spp. declining before Ha but populations stabilized, 2 native spp. stable populations	Colunga-Garcia and Gage 1998 ^a
Determine relative abundance and frequency of occurrence of coccinellids in nurseries	1986–1988	Maryland, USA	Adults collected during inspections of nurseries	28 spp. collected; Adults were collected from 67 locations (1986), 82 locations (1987), and 37 locations (1988); Relative abundance: C7>Co mac>H con>A2	Staines et al. 1990
Analyze population dynamics, species diversity; model potential of lady beetle community to suppress herbivores.	1989–2012	Michigan, USA	9 habitats; adults captured on yellow sticky cards changed every 2 wk over 14 wk during growing season	Yearly abundance varied widely; Increase in non-native species; >71% of adults were non-native; composition of lady beetle community changed during this 24-yr period, however, function remained similar over time period in agricultural and natural habitats.	Bahlai et al. 2013
Characterize populations of native and non-native coccinellid spp.; identify refuge habitats of native species.	2001–2006	S. Dakota, USA	Yellow sticky cards, timed visual observations and hand counts; 2–4 samples/mo, May–Aug.; larvae and adult lady beetles; aphid densities estimated	Ha & C7 larval majority. Ad. Ha & C7 present in low numbers in most habitats; A2 in western SD; no C9 or C. trans found	Hesler and Kieckhefer 2008
Determine whether lady beetle community structure in 3 agricultural crops was altered by C7 invasion	1973–1985 vs. 1988–1992	S. Dakota, USA	alfalfa, small grains, maize fields; sweep netting adults weekly in alfalfa and small grains; weekly visual samples in maize; avg. annual abundance from weekly samples	Structure of native lady beetle community differed before/after C7 arrival; Reduced abundance of C tra, A2; Adding C7 did not increase total abundance; levels of biological control unaffected	Elliott et al. 1996
Document changes in composition of native lady beetle community in Missouri over 118 yr; Determine if major shift in native species composition correlated with appearance of C7 and Ha	118 yr	Missouri, USA	Adults from museum collections; information from citizen science based Lost LadyBug Project; Data analyzed as multi-year datasets	Gradual change in community of native spp. during 20th century; No recent change in community composition attributed to C7 and Ha. Authors do not exclude an effect of non-native species on declines of native species.	Diepenbrock et al. 2016

Table 2. Continued

Goals/hypothesis/objectives	Study period	Location	Habitat, sampling methods, and life stages collected	Results and conclusions	Reference
Document relative abundance of native <i>Cyc sang</i> before/after Ha arrival in citrus orchards	1997–1998 vs. 2000–2001	Florida, USA	Before vs. after Ha arrival; Visual counts of adults on trees; 19 samples; 5 counties in Florida	Relative abundance of Ha increased; relative abundance of <i>C. sang</i> decreased	Michaud 2002
South America Document invasion of Ha in Chile; assess changes in native species in alfalfa	2010–2014	Chile	Sampled adults using 5 sticky cards/field; 10–18 commercial fields; one sample period in spring	10 native and 8 non-native spp.; non-native more abundant; 2012: Ha most common sp. Decrease in sp. richness and diversity with Ha increase.	Greze et al. 2016

Studies were typically designed to compare abundance of native species before and after the establishment of *Coccinella septempunctata* and/or *Harmonia axyridis*. Data are organized by continent, then by geographical latitude.

A2, *Adalia bipunctata*; A10, *Adali impunctata*; Ca14, *Calvia quatuordecimpunctata*; C7, *Coccinella septempunctata*; C5, *Coccinella quinquepunctata*; C9, *Coccinella novemnotata*; C. tra, *Coccinella transversoguttata*; C3, *Coccinella trifasciata*; Co. mac, *Coleomegilla maculata*; Cyc. San, *Cycloneda sanguinea*; Ha, *Harmonia axyridis*; H. con, *Hippodamia convergens*; H5, *Hippodamia quinquesignata*; H sin, *Hippodamia sinuata*; H13, *Hippodamia tredecimpunctata*; P14, *Propylea quatuordecimpunctata*.

^aThis is a 10-yr portion of data analyzed by Bahlai et al. (2013).

empirical data, IGP among aphidophagous coccinellids is predicted to be a rare event under field conditions (Kindlmann and Houdkova 2006); these authors suggest detailed field studies to quantify the occurrence and effects of IGP on multi-species interactions.

2) Competitive Exploitation

Based on a 24-yr study of native and non-native coccinellids at a Long Term Ecological Research (LTER) site in Michigan, USA, Bahlai et al. (2015) concluded that competitive exploitation was the likely mechanism involved in declines of two native species. A recent analysis of this Michigan dataset showed that the stable community abundance of lady beetles was due to yearly variation in competition between native and non-native species (Lamb et al. 2020). The authors caution that stability may not persist if the abundance of native species continues to decline. Evans (2000) hypothesized that the increasing abundance of *C. septempunctata* in alfalfa fields in Utah would result in increased competition among larvae for food resulting in smaller adult body sizes of native species. However, 9 yr of field data (1991–1999) during which the relative abundance of *C. septempunctata* increased from 5 to 95% did not cause a decrease in adult body size of five native species (Evans 2000). On the other hand, exploitative interspecific competition was an important mechanism explaining the high relative abundance of *H. axyridis* and declines of native and non-native species of coccinellids in Chile (Zaviezo et al. 2019).

3) Habitat Compression

This type of interaction between native and non-native Coccinellidae was documented in alfalfa fields and native habitats in Utah, USA (Evans 2004), but not in potatoes and native habitats in Maine, USA (Finlayson et al. 2008). Similarly, perennial grasslands in Missouri, USA serve as an important habitat for native species of lady beetles; and relatively few non-native species were observed in these habitats (Diepenbrock and Finke 2013).

These hypotheses are not mutually exclusive and in many systems there may be multiple mechanisms involved in the interactions between native and non-native species. For example, both exploitative competition and habitat compression were invoked to explain the interactions among non-native and native species over 24 yr at the LTER site in Michigan (Bahlai et al. 2015). To explain these interactions a fundamental understanding of the dynamic nature of coccinellid communities is required. The relative abundance of individual species within a community can show significant year-to-year variation (Elliott et al. 1996, Honek et al. 2014); consequently short-term (<3 yr) field studies need to be interpreted with caution. Sampling frequency for these interactive studies varies from weekly to monthly to 1 yearly sample at a given location (Table 2). Having a fundamental understanding of the seasonal variation in community composition is required to interpret sampling data and the interactions between native and non-native species (Honek et al. 2015, 2017, 2019).

Impacts on Biodiversity

Several studies, based on museum records and long-term comparisons of distribution records indicate that the diversity of native Coccinellidae has declined in North America during the late 20th and early 21st centuries (Harmon et al. 2007, Diepenbrock et al. 2016). Long-term gradual declines in several coccinellid species also occurred in the United Kingdom (Brown and Roy 2018) and the Czech Republic (Honek et al. 2016). Contributing factors include landscape-scale changes, climate change, reductions in prey densities,

Table 3. Field studies documenting cannibalism and/or IGP in Coccinellidae

Region, Species ^a	Habitat/location	Sampling Method	Results and Conclusions	Reference
Asia				
Ha, C7	Hibiscus tree stand, Japan	Daily observation/life table	Results: during aphid scarcity, Ha L4 ^b survived more than C7; Ha L4 with highest IGP and cannibalism; Ha > C7 IGP asymmetry Conclusion: prey abundance influences cannibalism and IGP.	Hironori and Katsuhiko 1997
Ha, C7, Pj	Cotton field, N. China	Field collection/molecular gut content analysis	Results: DNA-based gut-content analysis; the overall detection rate in predator-prey: 9.1% in C7-Pj, 26.7% in Ha-Pj, 0% in Pj-C7, 0.6% in Ha-C7, 53.2% in Pj-Ha, and 72.7% in C7-Ha.	Yang et al. 2017
Ha	Botanical garden, Kyoto, Japan	Daily observation/ Life table analysis	Results: 20% nonsibling cannibalism; 30% sibling cannibalism; 9.8–20.3% pupal cannibalism Conclusion: Cannibalism important for population stability and persistence.	Osawa 1993
North America				
Ha, C7, P14, vs. native Cmac	Soybean fields, Quebec, Canada	Sweep net samples, Molecular gut analysis of larvae	Results: IGP high among L4; 47–59% L4 larvae with DNA of other species; Cmac IG prey (sometimes rare)	Gagnon et al. 2011
Europe				
Ha larvae vs. eggs of A2, <i>Oenopia conglobata</i> (native spp.)	Linden trees, N. Italy	Molecular gut analysis of larvae	Results: 1.5% tested larvae had A2 egg DNA; 5% <i>O. conglobata</i> egg DNA	Rondoni et al. 2015
Native species vs. C7, Hvar	Melons, Italy	Field collections, Molecular gut analysis of larvae	Results: IGP levels approx. 20–25 % for both species; field levels of IGP by C7 lower than in lab	Rondoni et al. 2018
Ha	Linden trees, Brussels, Belgium	Testing for exogenous alkaloids	Results: 20.5% Ha L3–L4 ^b with alkaloids of native coccinellids; positives from 95% of sites studied, quantity often >30%; alkaloids from <i>Adalia</i> spp, <i>Calvia</i> spp and P-14 found	Hautier et al. 2011
Ha vs. A2, A10	Linden trees, Eastern England	Molecular gut analysis of larval for <i>Adalia</i> DNA	Results: 7.7% Ha larvae with A2, 4.5% with A10 DNA Conclusion: IGP—related to declines in native lady beetles	Thomas et al. 2013
Ha vs. A2, A10, Ebal, Chcar	Various locations in England, France, Germany, Slovakia, Czech Republic	Molecular gut analysis of larvae	Results: 9.6 % Ha larvae with A2, 2.8 % with A10, 2.8% with Ebal DNA; none with Chcar	Brown et al. 2015
South America				
Ha, Hvar, Hcon, Er	Wheat fields, central Chile	Molecular gut analysis of adults and larvae	Results: 92% of coccinellid samples positive for IGP of at least one other species 43% of samples positive for two or three coccinellid species Native species Er most common intraguild prey, Ha least common intraguild prey Conclusion: IGP is common in this wheat system; native Er common IG prey	Ortiz-Martinez et al. 2020

^aA2, *Adalia bipunctata*; A10, *Adalia decempunctata*; Ca14, *Calvia quatuordecimguttata*; Chcar, *Chrysopa carnea*; Cmac, *Coleomegilla maculata*; C7, *Coccinella septempunctata*; Ebal, *Epiplatys balearicus*; Er, *Eriopis chilensis*; Ha, *Harmonia axyridis*; Hvar, *Hippodamia variegata*; P14, *Propylaea quatuordecimpunctata*.

^bL3, L4: third and fourth instar larvae.

and/or the presence of non-native species; there has not been any consistency in the strength of these factors (Harmon et al. 2007, Honek et al. 2014). For example, Diepenbrock et al. (2016) documented that the lady beetle community in Missouri has gradually changed over time with no sudden shift in species composition following the recent appearance of *C. septempunctata* and *H. axyridis*. Comparing detailed records from Gordon (1985) and current information from the citizen-science based Lost Lady Beetle project (www.lostladybug.org) also indicate that the ranges of many native coccinellid species in North America have contracted. Some caution is required to interpret these changes, however, because Gordon's (1985) summary is based on museum records and taxonomic expertise, while recent data are from citizen science-based observations from 2012 to the present. Differences might be expected given how the information on distributions were collected using two different methods separated by almost three decades (Gordon 1985, Gardiner et al. 2012).

Displacement of a native species could result in a reduction in biodiversity, but at what scale? If a non-native displaces more than one species, local biodiversity is reduced, but if the displacement is one-for-one, biodiversity is unchanged at a local scale (the same number of species is present). If the displacement causes the extinction of the native species, the consequence is a reduction in global (but not local) biodiversity. In discussing declines in native (or extant) species, authors often conclude that this is a reduction in biodiversity, but frequently do not specify the scale at which this occurs and argue that such reductions necessarily reduce biological control services. Importation (classical) biological control efforts often focus on establishing highly specific natural enemies, and when successful this may result in a reduction in native generalists that may opportunistically feed on the target species. The resultant shift in relative abundance among members of these guilds is not considered a reduction in biodiversity (Kindlmann et al. 2017), although similar processes are at play. To maintain a diverse natural enemy community that is often sought in conservation biological control programs, such diversity also increases the probability of competition, IGP, and functional redundancy (Cardinale et al. 2003, Straub et al. 2008, Straub and Snyder 2008, Jonsson et al. 2017, Ortiz-Martinez et al. 2020).

Effects on Levels of Biological Control

The disruption/displacement of native coccinellids by non-native species has been the focus of most studies over the past two decades (e.g., Turnock et al. 2003; Roy et al. 2012; Bahlai et al. 2013, 2015; Grez et al. 2016). However, studies describing shifts in relative abundance among coccinellid species frequently do not measure nor even mention changes in prey abundance or diversity. While some claim that the majority of displacements results in negative outcomes (e.g., Reitz and Trumble 2002), the displacement of existing but ineffective natural enemies is a common result in successful classical biological control programs, leading to reductions in target prey densities (Salas Gervassio et al. 2017). Therefore, it should not be surprising that reductions of native coccinellids by non-native invasive coccinellids would result in reduced densities of common prey or no change in prey density (Snyder and Tylanakis 2012). Both of these outcomes have been observed in the few systems evaluated where *H. axyridis* or *C. septempunctata* have displaced native coccinellids. Prey (three aphid species) densities significantly declined in potatoes after the establishment of *H. axyridis* and reductions in native predator abundance were documented in a 31-yr study in Maine (Alyokhin and Sewell 2004; see discussion of these results in Kindlmann et al. 2011). Similarly, in West Virginian apple orchards, *H. axyridis* has negatively interacted with *C. septempunctata*, but provided higher levels of *Aphis spiraeicola* Patch (Hemiptera:

Aphididae) control (Brown and Miller 1998; Brown 2003, 2004). In North American hemlock forests, *H. axyridis* provides predation during summer, complementing predation of the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) by the non-native coccinellid *Sasajiscymnus* (*Pseudoscymnus*) *tsugae* Sasaji (Coleoptera: Coccinellidae) (Flowers et al. 2006). Following releases of *H. axyridis* for aphid suppression in Georgia pecan orchards, Tedders and Schaefer (1994) reported that by 1992, *H. axyridis* was the dominant coccinellid (54%), which was correlated with reduced aphid densities.

In a review of the role of *H. axyridis* in biological control of the soybean aphid (*Aphis glycines*) Matsumura (Hemiptera: Aphididae) in North America, Koch and Costamagna (2017) summarized studies documenting the role of *H. axyridis* in preventing and suppressing *A. glycines* outbreaks. Based on their review, the negative effects (e.g., IGP) of *H. axyridis* on native species do not necessarily cause reduced levels of aphid control (Koch and Costamagna 2017). Biological control of the soybean aphid in North America by *H. axyridis* has been considered an example of invasional reconstruction by Snyder and Evans (2006) due to the presence of the non-native complex: a non-native agricultural crop, an overwintering host plant, an invasive aphid species, and *H. axyridis* (Ragsdale et al. 2011). In cotton fields in Arkansas, *C. septempunctata* contributes to biological control, interacting with several native species in the suppression of the cotton aphid (*Aphis gossypii*) Glover (Hemiptera: Aphididae) (Conway and Kring 2010).

Interactions Within Native Range: Mechanisms of Coexistence

Harmonia axyridis and *C. septempunctata* are both widely distributed and relatively abundant predatory species in a wide range of agricultural systems in their native range. In Asia, the distribution of *H. axyridis* extends from Siberia to central Asia and Vietnam; it can be commonly found in eastern China, Japan, Korea, and Mongolia (Ren et al. 2009, Orlova-Bienkowskaja et al. 2015, CABI Invasive Species Compendium (<https://www.cabi.org/isc/datasheet/26515>)). *Coccinella septempunctata* occurs throughout Eurasia and is widely distributed in China (Ren et al. 2009, CABI Invasive Species Compendium (<https://www.cabi.org/isc/datasheet/11733>)). Given this broad geographic overlap, these two predatory species have a long history of coexistence within their native ranges. With a third widely distributed native lady beetle in Asia, *Propylea japonica* (Thunberg), these three species are often the most abundant members of aphidophagous guilds in a variety of habitats (Table 4). These habitats include annual crops: wheat (Li et al. 2011), maize (Wang et al., 2013), cotton (Wang et al. 2013), tobacco (Gao et al. 2012), and soybean (Liu et al. 2012), and perennial trees and shrubs such as tea and fruit orchards (Han and Chen 2001) in China, and a variety of trees in Japan (Yasuda and Kimura 2001, Toda and Sakuratani 2006). *Harmonia axyridis* often coexists with *C. septempunctata* or *P. japonica* in the same habitat yet their relative abundances differ (Table 4). While *H. axyridis* can be more abundant than other lady beetles in some habitats, its dominance is replaced by other species in a different habitat; the dominance can also show seasonal variation (Table 4). The mechanisms underlying the coexistence of these three species remain largely unknown and require additional research.

Five species of predatory coccinellids have been introduced from other continents into Asia, mostly as biological control organisms, and their current distribution remains localized (Table 1). The interactions of these non-native species with native coccinellids has not been studied in China. *Adalia bipunctata* L. (Coleoptera:

Table 4. Relative abundances of most common lady beetles and other species in the same guild in different habitats within their native range

Country/Location/Region	Habitat	Most common predator species	Relative abundance of the most common species ^a	Methods	Reference
China					
Shenyang city, Liaoning Province	Maize	<i>H. axyridis</i> , <i>P. japonica</i> , <i>Chrysopa sinica</i> , <i>Ch. septempunctata</i> + 3–5 other spp.	1980: Chse (35.8%) > Chs (30.7%) > Ha (15.4%) > Pj (6.1%) 1981: Ha (53.5%) > Pj (8.9%) > Chs (2.9%) > Chse (2%) 1982: Ha (13.8%) > Pj (6.1%) > Chs (0.7%) > Chse (0.3%)	3-yr field survey; calculation methods unavailable.	He et al. 1996
Langfang city, Hebei Province	Maize	<i>H. axyridis</i> , <i>P. japonica</i>	Pj (67%) > Ha (33%)	1-yr survey; relative abundance estimated from figures.	Wang et al. 2013
Langfang city, Hebei Province	Cotton	<i>H. axyridis</i> , <i>P. japonica</i>	Pj (53%) > Ha (47%)	1-yr survey; relative abundance estimated from figures.	Wang et al. 2013
Harbin city, Heilongjiang Province	Sorghum	<i>H. axyridis</i> , <i>P. japonica</i> , <i>Ch. sinica</i> .	2012: Chs (37.5%) > Ha (35.0%) > Pj (27.5%) 2013: Chs (43.9%) > Pj (29.4%) > Ha (26.7%)	2-yr survey; no. individuals/100 plants across season.	Shao et al. 2014
Wang Jiang county, Anhui Province	Cotton	<i>H. axyridis</i> , <i>C. septempunctata</i> , <i>P. japonica</i> , + several spiders	Pj (92.8%) > Ha (5.0%) > C7 (2.0%)	1-yr survey across cotton-growing season. Seasonal totals.	Zhu et al. 2002
Taian city and surroundings, Shandong Province	Wheat	<i>H. axyridis</i> , <i>C. septempunctata</i>	Whereas the two lady beetles were similar in densities during the first 7 yr but from then on C7 was obviously more abundant than Ha.	26-yr (1991–2016) data; yearly totals	Liang 2017
Langfang city, Hebei Province	Wheat	<i>P. japonica</i> , <i>C. septempunctata</i> , <i>Ch. septempunctata</i> + minor spp.	Ha (58%) > C7 (33%)	2-yr survey at 10 d intervals during crop season; ranking by dominance	Wang et al. 2012
Langfang city, Hebei Province	Soybean	<i>P. japonica</i> , <i>C. septempunctata</i> + minor spp.	Pj (0.68) > C7 (0.19)	2-yr survey at 10 d intervals during crop season; ranking by dominance	Wang et al. 2012
Langfang city, Hebei Province	Sweet melon & chilli	<i>P. japonica</i> , <i>H. axyridis</i> + minor spp.	Pj (0.64) > Ha (0.28)	2-yr survey at 10 d intervals during crop season; ranking by dominance	Wang et al. 2012
Langfang city, Hebei Province	Tree windbreak	<i>H. axyridis</i> , <i>C. septempunctata</i> + minor spp.	C7 (0.54) > Ha (0.44)	2-yr survey at 10 d intervals during crop season; ranking by dominance	Wang et al. 2012
Langfang city, Hebei Province	Nursery garden	<i>P. japonica</i> , <i>H. axyridis</i> + minor spp.	Pj (0.73) > Ha (0.17)	2-yr survey at 10 d intervals during crop season; ranking by dominance	Wang et al. 2012
Langfang city, Hebei Province	Plum orchard	<i>P. japonica</i> , <i>H. axyridis</i> + minor spp.	Pj (0.74) > Ha (0.22)	2-yr survey at 10 d intervals during crop season; ranking by dominance	Wang et al. 2012
Pudong district, Shanghai	Fruit orchards	12 coccinellid spp.	Pj (40.1%) > <i>Menocheilus sexmaculatus</i> (22%) > Ha (17.3%) > C7 (16.7%)	1-yr sampling on seven fruit orchards; relative abundance	Zhao et al. 2020

Table 4. Continued

Country/Location/Region	Habitat	Most common predator species	Relative abundance of the most common species ^a	Methods	Reference
Gaoligong National Park, Qinghai-Tibetan plateau, Yunnan Province	Mountains	56 coccinellid spp.	C7 (20.5%) > <i>H. eucharis</i> (17%) > <i>Oenopia kerbi</i> (5.3%) > <i>Ha</i> (0.9%)	1-yr survey; relative abundance	Wu et al. 2011
Japan					
Kyoto, Botanical garden (1 ha area)	<i>Salix sieboldiana</i> <i>Typha angustifolia</i> <i>Prunus persica</i> <i>Sambucus sieboldiana</i> <i>Spiraea thunbergii</i> & <i>S. blumei</i> <i>Salix korriyanagi</i>	<i>H. axyridis</i> , <i>C. septempunctata</i> , <i>P. japonica</i> , + 2 coccinellid spp.	C7 (69%) > <i>Ha</i> (18%) > <i>Pj</i> (6%), C7 (69%) > <i>Ha</i> (18%) > <i>Pj</i> (7%), <i>Ha</i> (43%) > C7 (12%) > <i>Pj</i> (8%), <i>Ha</i> (33%) > C7 (11%) > <i>Pj</i> (5%), <i>Ha</i> (54%) > C7 (2%) = <i>Pj</i> (2%), <i>Ha</i> (85%) > C7 (10%) > <i>Pj</i> (2%)	3-yr sampling on six tree species/genus. Relative abundance	Osawa 2010

^aHa, *Harmonia axyridis*; C7, *Coccinella septempunctata*; *Pj*, *P. japonica*; Chs, *Chrysopa sinica*; Chse, *Chrysopa septempunctata*.

Coccinellidae), after an unintentional introduction into Japan (Sakuratani et al. 2000), has slowly expanded its range. It reduces competition with *H. axyridis* by separation in time (desynchronization) and with *C. septempunctata* by habitat segregation (Toda and Sakuratani 2006), even though it overlaps with them in habitats and prey species (Kajita et al. 2000). Asymmetric IGP by native *H. axyridis* is also tentatively suggested as a potential factor slowing the expansion of *A. bipunctata* (Sakuratani et al. 2000, Ware et al. 2009).

Species coexistence can be maintained by various stabilizing mechanisms, including resource partitioning, frequency-dependent mortality by natural enemies (including cannibalism and IGP), and fluctuations in population densities and variation in environmental factors in space and time (Chesson, 2000). Even though lady beetles in their native range have been a focus of research, mainly because of their roles as biological control organisms in agroecosystems; little attention has been directed to mechanisms explaining the coexistence of *H. axyridis*, *C. septempunctata*, and *P. japonica*. Here we discuss possible mechanisms of their coexistence within their native ranges.

Resource Partitioning

Harmonia axyridis, *C. septempunctata*, and *P. japonica* have different ranges of aphids that are suitable prey (sensu Hodek (Hodek et al. 2012)), and/or prey threshold densities needed for successful individual development and reproduction. *Coccinella septempunctata* is not as polyphagous as *H. axyridis*, whose diet includes scores of aphid species and which can also successfully develop and/or reproduce on non-aphid food such as pollen (Berkvens et al. 2008), moth eggs (Schanderl et al. 1988, Abdel-Salam and Abdel-Baky 2001), pupae of the parasitoid *Trichogramma* sp. (Guo and Wan 2001), or drone bee powder (Nijima et al. 1986). For example, a field survey in an organic peach orchard with an undergrowth of alfalfa *Medicago sativa* L. and *Lagopsis supina* (Labiatae) in a suburb of Beijing, China, found direct correlations between densities of lady beetle predators and selected aphid species; *P. japonica* densities were tied to *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) while *C. septempunctata* was linked to *Tuberocephalus momonis* (Matsumura) (Hemiptera: Aphididae) (Dong et al. 2011).

Different lady beetle species may require species-specific minimum prey densities to sustain population growth. Under laboratory conditions, coexisting *H. axyridis* and *C. septempunctata* populations maintained similar growth patterns at high aphid densities. However, when aphid prey was insufficient, the *H. axyridis* population continued to grow, while the *C. septempunctata* population declined within 30 d (Liu and He 2008). The different population growth patterns observed for *H. axyridis* and *C. septempunctata* were explained by their different prey density threshold requirements (Liu and He 2008).

Interactions Within the Guild of Predatory Coccinellidae

To determine the role of *H. axyridis* in aphidophagous guilds, a survey from April to August of all adult predators of aphids at multiple sites (with seven species of plants and eight aphid species) in Japan documented a negative relationship between the proportion of *H. axyridis* and five coexisting aphidophagous coccinellids (Osawa 2011). IGP in favor of *H. axyridis* has been frequently shown in numerous laboratory experiments and field observations in Asia, but its role in maintaining coexistence of these species remains open to debate. The IGP advantage of *H. axyridis* in its invaded range (Lucas 2005, 2012; Mirande et al. 2015) also

appears to be present in its native range (e.g., Sato et al. 2009, Guo et al. 2016). The observed asymmetric IGP favoring *H. axyridis* in laboratory studies supports field observations (e.g., Yang et al. 2017; Table 3). For example, a 2-yr field observation of coexisting *H. axyridis* and *C. septempunctata* on *Hibiscus syriacus* L. trees in Japan showed that survival of *H. axyridis* fourth instars was higher than that of *C. septempunctata* when their *Aphis gossypii* prey was scarce, owing to the high frequency of intra- and inter-specific predation (Hironori and Katsuhiko 1997). Although *H. axyridis* has a distinct advantage over its competitors in a guild, the incidence of IGP may not be prevalent due its different habitat preference and predilection for cannibalism (Osawa 2011). Cannibalism by *H. axyridis* was estimated to be 50% on eggs (Osawa 1993) and 14.4% on pupae in the field in Japan (Osawa 1992). It is assumed that cannibalism operates as an effective stabilizing and self-regulatory mechanism to limit *H. axyridis* population growth, leading to its coexistence with other lady beetles (Osawa 2011). In addition, early emigration of *C. septempunctata* larvae may enable them to escape IGP by *H. axyridis* (Sato et al. 2003). We assume that IGP and cannibalism interact to maintain the coexistence of *H. axyridis* with members of the guild of predatory coccinellids. However, additional research is needed to focus on the influence these coexistence mechanisms have on biological control of pest populations.

Differences in Seasonal Dynamics and Spatial Occurrence

Differences in seasonal dynamics among species of lady beetles in a habitat may contribute to the coexistence of different species (Lu et al. 2015). The two lady beetles, *P. japonica* and *H. axyridis*, coexist as dominant predators in multiple farming systems in northern China, but their phenological peaks differ. In cotton fields, *P. japonica* occurs during the early and middle periods of cotton growth, whereas *H. axyridis* appears at a later growth stage (Wang et al. 2013). A similar dynamic was also observed on *Hibiscus syriacus* trees in Japan, where *C. septempunctata* starts oviposition earlier than *H. axyridis* (Yasuda and Shinya 1997). In soybean fields in Heilongjiang Province of northeast China, *H. axyridis* reaches its seasonal abundance peak later than *P. japonica* (Liu et al. 2012). In sorghum fields, *H. axyridis* reaches its abundance peak later than *P. japonica* and the lacewing *Chrysopa sinica* Tiedt (Neuroptera: Chrysopidae) (Shao et al. 2014). In a survey of lady beetles in a landscape, with multiple annual crop fields separated by tree hedges in Hebei Province of Northern China, both *P. japonica* and *C. septempunctata* were much more abundant than *H. axyridis* in the hedges and crop fields (Wang et al. 2012). In maize fields, *H. axyridis* is more abundant at field margins while *P. japonica* dominates in the field centers (Liu et al. 2012).

In natural habitats, *H. axyridis* tends to prefer trees and shrubs, whereas *C. septempunctata* frequently occurs in grassy habitats (Osawa 1992, Hironori and Katsuhiko 1997). It is hypothesized that the coexistence of *H. axyridis* with other lady beetles in largely attributed to its high searching capacity and versatility in exploiting heterogeneous and temporary habitats, coupled with density-dependent and self-regulatory population regulation (e.g., cannibalism) (Osawa 2011).

Biotic Mortality Factors

Differential impacts of natural enemies on different lady beetles can also contribute to their coexistence. In a laboratory study in Japan, all *C. septempunctata* larvae, an intermediate number of *P. japonica*, but no *H. axyridis* were attacked and eaten by the crab spider *Misumenops tricuspidatus* (F.) (Araneae: Thomisidae) (Yasuda and

Kimura 2001). Numerous parasitoids attack predaceous lady beetles, but the levels of parasitism are little known (Ceryngier et al. 2012). *Coccinella septempunctata* and *H. axyridis* often coexist in the same habitat, but their parasitoid loads (total number of parasitoid species) and parasitism pressure can vary widely. A 2-yr survey of parasitoids of *H. axyridis* and *C. septempunctata* in agricultural ecosystems in the rural suburbs of Nanjing, Eastern China showed that *H. axyridis* was parasitized by two species of parasitoids, one unique (a phorid fly *Phalacrotophora* sp. probably *P. phylaxyridis* (Diptera: Phoridae)) and another (*Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae), an adult parasitoid) shared with *C. septempunctata*. *Coccinella septempunctata* was attacked by eight species (H.-T. Song, personal communication). *Oomyzus scaposus* (Thomson) and *O. spiraculus* Song, Fei & Cao (Hymenoptera: Eulophidae), are common parasitoids of *C. septempunctata*, but rarely attack *H. axyridis* (Song 2017; Song et al. 2017, 2020). In Western Siberia, the phorid parasitoid *P. fasciata* parasitized 45% of *C. septempunctata* compared with 25–30% of *H. axyridis* (Filatova 1974). In Honshu, Japan, the braconid *Dinocampus coccinellae* caused 50% parasitism of *C. septempunctata* adults but only 20% of *H. axyridis* individuals (Koyama and Majerus 2008). Aphidophagous coccinellids seem to suffer lower rates of parasitism than coccidophagous or herbivorous species, likely due to their higher mobility (Riddick et al. 2009).

In addition to predators and parasitoids, parasites (e.g., fungi, mites, and nematodes), though not lethal to their hosts, may indirectly impact the coexistence of coccinellids. The obligate ectoparasite fungus *Hesperomyces virescens* Thaxter (Laboulbeniales: Laboulbeniaceae), which infects 30 species of lady beetles on all continents except Antarctica, was discovered on museum specimens of *H. axyridis* from China (Haelewaters et al. 2014). Mites and nematodes frequently infect *H. axyridis* in Asian Russia (Kuznetsov 1997), but parasite infections of *H. axyridis* and *C. septempunctata* in China remain poorly known (Haelewaters et al. 2017).

Comparative Studies to Quantify Differences in Native and Non-Native Populations

Life History Traits of *H. axyridis*

A question that has received increased attention is modification of *H. axyridis* life history traits in invaded regions compared with populations from the native range (Sloggett 2012, Lombaert et al. 2014, Raak-van den Berg et al. 2017, Li 2020). Changes in life history characteristics may contribute to invasion success (van Kleunen et al. 2010, Colautti and Lau 2015, Dlugosch et al. 2015). For example, *H. axyridis* individuals from the invaded region in Russia show significantly higher propensity for larval cannibalism than those from the native Caucasian region (Ovchinnikova et al. 2019). A comparison of photoperiodic regulation of reproductive diapause in *H. axyridis* between two invasive (Czech Republic and Sochi) and native populations of *H. axyridis* from Siberia and South Korea, documented that invasive *H. axyridis* individuals decreased their sensitivity to photoperiod and this continued to change during the invasion (Reznik et al. 2015). A meta-analysis of life history traits of *H. axyridis* populations from Europe, North America, and Asia indicated that several life history traits of *H. axyridis* have changed during the invasion: the preoviposition period became shorter, fecundity at low temperatures increased, and longevity was extended at all temperatures (Raak-van den Berg et al. 2017). Similarly, the common haplotype of *H. axyridis* in North America performs better in its developmental and reproductive parameters than the same *H. axyridis* haplotype in the native range (Li 2020).

Genetic Diversity and Differentiation of *H. axyridis*

Analysis of mitochondrial CO1 of *H. axyridis* showed significant differences between the eastern and western populations in the native Russian range, suggesting that all populations in the invaded North American and European regions originated from populations from eastern Asia (Blekhnman et al. 2020). Examination of single-copy nuclear genes of *H. axyridis* populations across mainland China and North America, South America, and Europe indicated that the genetic diversity in China was higher than that in North America and Europe, but lower than that in South America (Li 2020). In addition, this analysis suggests that there is significant gene flow between Chinese and North American or European populations, but less between Chinese and South American populations (Li 2020). Genetic factors play a key role in determining the multicolored morph patterns in *H. axyridis* (Gautier et al. 2018). A comparison in color morphs of *H. axyridis* between its native and invaded ranges may suggest mechanisms for its invasiveness outside its native range (Honek et al. 2020b).

Prevalence of Maternally Inherited Bacteria Associated with *H. axyridis*

Over 50% of 21 examined lady beetle species harbor maternally inherited bacteria, i.e., *Wolbachia*, *Rickettsia*, and *Spiroplasma* (Weinert et al. 2007). Endosymbiotic microorganisms inhabiting *H. axyridis* may confer fitness benefits to their hosts, contributing to invasion success. *Spiroplasma*-infected *H. axyridis* adults are larger and females possess more ovarioles than uninfected individuals, which could potentially increase fecundity (Elnagdy et al. 2013). An examination for *Rickettsia* and *Spiroplasma* in *H. axyridis* populations from seven localities in its native range (six in Russia and one in Japan) and six from the invaded ranges (five from central Europe and one from North America) found a consistently low (0.03%) *Rickettsia* infection in both the native and non-native ranges, but *Spiroplasma* was only detected in populations from the native range (Goryacheva et al. 2017). *Spiroplasma* infections in native *H. axyridis* populations in Japan and Russia vary from 2 to 60% of individuals (Majerus et al. 1998, Zakharov et al. 1999, Tsushima et al. 2015, Goryacheva et al. 2017). A recent extensive examination of *H. axyridis* populations from 30 geographical localities across mainland China and 9 from North America diagnosed *Wolbachia* infections in both native and invaded ranges, but *Spiroplasma* infections were only detected in the native range, and no *Rickettsia* infection was found (Li 2020).

Conclusions

Even though numerous studies examined the spatial and temporal patterns among predatory coccinellids in their native range in Asia, our understanding of mechanisms involved in the coexistence of these species remains limited. Thus, our consideration of species coexistence in the native ranges does not allow us to critically address the question ‘Is there evidence that non-native lady beetle species have different ecological effects in their native vs. non-native ranges?’ Finding out why and how they coexist may provide useful information about characteristics that allow species to find ways of coexisting with these aggressively dominant species. We could then identify the necessary traits and determine if they are present in the species native to the newly invaded areas. This has not yet been done during the extensive research concerning these invasive species.

Given the relatively few non-native species established in Asia (Table 1), there has been less research on interactions between native and non-native species than in the Americas or Europe. Prior to

the appearance of the non-native species, *C. septempunctata* and/or *H. axyridis*, in these regions, there were relatively few studies quantifying interactions and relative abundances of native predatory coccinellids (e.g., Honek and Rejmanek 1982, Lovei et al. 1991, Nedved 1999; summary in Honek 2012). Several of these early studies examined the role of multiple coccinellid species in temporal and/or spatial dynamics of predator–prey interactions and levels of biological control (Kring and Gilstrap 1986). The importance of studying the predatory larval stages of coccinellids was emphasized by Lovei et al. (1991); one of the first studies to focus on larval interactions of native and non-native species in North America was Evans (1991). Prior to 1991, a Web of Science search using two key words (Coccinellidae and Interactions) returned only seven citations. From 1991 to 2020, 417 references were found based on these two key words, reflecting the increased research focus on interactions among native and non-native species following the spread of *C. septempunctata* and *H. axyridis* into new regions.

We are witnessing the potential global homogenization of the aphid feeding coccinellid fauna—primarily dominated by *H. axyridis* and *C. septempunctata* in many invaded regions. The declines in the relative abundance of native species following the spread of non-native species are documented by several long-term studies (e.g., Evans 2004, Brown and Roy 2018, Honek et al. 2019, Lamb et al. 2019), which is of great concern for biodiversity and the persistence of native species. Is the global homogenization of the community of predatory coccinellids to be expected given the similarities in the worldwide production of a limited number of major agricultural crops and the global distribution of many species of aphids infesting these crops? Is a reduction in the biodiversity of predatory coccinellids feeding on aphids given these environmental conditions, to be expected? Natural and/or seminatural environments could be important refuges for native species (Bahlai et al. 2015, Evans 2017). For example, *Coccinella novemnotata* has been the focus of several papers due to its decline in North America (e.g., Harmon et al. 2007, Tumminello et al. 2015). But in a multi-year study, Evans (2017) documented that in the late 1980s and early 1990s, *C. novemnotata* and *C. septempunctata* were initially both relatively rare in Utah alfalfa fields. The relative abundance of *C. septempunctata* increased rapidly in subsequent years, but *C. novemnotata* persisted at low densities in alfalfa fields and natural and seminatural habitats (Evans 2017). We anticipate continued invasions by coccinellids across the continents, unfortunately providing new opportunities to explore global homogenization of the coccinellid fauna and its effects on biodiversity and biological control.

Multi-year ecologically based studies combined with molecular, genetic, and demographic modeling techniques to quantify population and food web dynamics and movement within landscapes in Asia would provide a better understanding of the mechanisms underlying coexistence of predatory coccinellids (Lawson Handley et al. 2011; Thomas et al. 2013; Heimoana et al. 2017; Brown and Roy 2018; Sethuraman et al. 2018, 2020; Ammann et al. 2020). This type of detailed knowledge of the native coccinellid community in Asia is critical to determine the potential effects of the invasive populations (biotypes) of *H. axyridis* from Europe that are spreading in Eurasia. This is based on the assumption that, the invasive European population of *H. axyridis* will continue to expand into western Russia and China (Poutsma et al. 2008, Orlova-Bienkowskaja et al. 2015). The European population of *H. axyridis* has genetic and life history characteristics that differ from native populations in eastern Russia and presumably the rest of Asia (Tayeh et al. 2014, Reznik et al. 2015, Goryacheva et al. 2017, Raak-van den Berg et al. 2017, Ovchinnikova et al. 2019, Li 2020). Hybridization has been demonstrated between a lab-selected flightless strain and

non-native *H. axyridis* in Europe, producing hybrids that developed faster and produced larger individuals capable of flight (Facon et al. 2011). The interactions and potential hybridization between native and non-native populations of *H. axyridis* in Asia are likely to be complex due to population differences in endosymbionts, parasite loads, and prey defenses (Gegner et al. 2015, Goryacheva et al. 2017, Goryacheva and Blekman 2017, Lenhart et al. 2018, Orlova-Bienkowskaja et al. 2018).

The potential effects of an expanding European *H. axyridis* population on interactions with existing native *H. axyridis* populations, sympatric *Harmonia* species (Rasekh and Osawa 2020) and native coccinellids in eastern Russia and Asia should be considered. For example, two Holarctic coccinellids, *Coccinella transversoguttata* Brown and *Hippodamia tredecimpunctata* L. (Coleoptera: Coccinellidae) seem to have declined in abundance in regions of North America (e.g., South Dakota and Maine) after the appearance of non-native species including *C. septempunctata* and *H. axyridis* (Elliott et al. 1996, Alyokhin and Sewell. 2004). These four species coexist in eastern Russia (Kuznetsov 1997), but the mechanisms involved are not known. Multi-national teams are needed to conduct comparative studies not only in the invaded regions, but critically in the native ranges of these species.

Acknowledgments

We thank the China Scholarship Council for a scholarship supporting H. Li's research in the Department of Entomology at the University of Kentucky. This work was supported by the National Key R&D Program of China (2017YFE0104900, to B. Li). J.J.O. was supported by the National Institute of Food and Agriculture, United States Department of Agriculture, Hatch Program under accession number 1008480.

References Cited

- Abdel-Salam, A. H., and N. F. Abdel-Baky. 2001. Life table and biological studies of *Harmonia axyridis* Pallas (Col., Coccinellidae) reared on the grain moth eggs of *Sitotroga cerealella* Olivier (Lep., Gelechiidae). *J. Appl. Entomol.* 125: 455–462.
- Alyokhin, A., and G. Sewell. 2004. Changes in a lady beetle community following the establishment of three alien species. *Biol. Invasion.* 6: 463–471.
- Ammann, L., R. Moorhouse-Gann, J. Cuff, C. Bertrand, L. Mestre, N. P. Hidalgo, A. Ellison, F. Herzog, M. H. Entling, M. Albrecht, et al. 2020. Insights into aphid prey consumption by ladybirds: optimising field sampling methods and primer design for high throughput sequencing. *PLoS One.* 15: e0235054.
- Bahlai, C. A., M. Colunga-Garcia, S. H. Gage, and D. A. Landis. 2013. Long-term functional dynamics of an aphidophagous coccinellid community remain unchanged despite repeated invasions. *PLoS One.* 8: e83407.
- Bahlai, C. A., M. Colunga-Garcia, S. H. Gage, and D. A. Landis. 2015. The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. *Biol. Invasion.* 17: 1005–1024.
- Bell, J. R., D. Blumgart, and C. R. Shortall. 2020. Are insects declining and at what rate? An analysis of standardised, systematic catches of aphid and moth abundances across Great Britain. *Insect Conserv. Divers.* 13: 115–126.
- Berkvens, N., J. Bonte, D. Berkvens, K. Deforce, L. Tirry, and P. D. Clercq. 2008. Pollen as an alternative food for *Harmonia axyridis*. *Biocontrol.* 53: 201–210.
- Blekman, A., I. Goryacheva, D. Schepetov, and I. Zakharov. 2020. Variability of the mitochondrial CO1 gene in native and invasive populations of *Harmonia axyridis* Pall. comparative analysis. *PLoS One.* 15: e0231009.
- Brown, M. W. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl.* 48: 141–153.
- Brown, M. W. 2004. Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA. *Biol. Contr.* 29: 189–198.
- 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: 143–151.
- Brown, P. M. J., and H. E. Roy. 2018. Native ladybird decline caused by the invasive harlequin ladybird *Harmonia axyridis*: evidence from a long-term field study. *Insect Conserv. Divers.* 11: 230–239.
- Brown, P. M. J., C. E. Thomas, E. Lombaert, D. L. Jeffries, A. Estoup, and L. J. Lawson Handley. 2011. The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. *BioControl.* 56: 623–641.
- Brown, P. M. J., B. Ingels, A. Wheatley, E. L. Rhule, P. de Clercq, T. van Leeuwen, and A. Thomas. 2015. Intraguild predation by *Harmonia axyridis* (Coleoptera: Coccinellidae) on native insects in Europe: molecular detection from field samples. *Entomol. Sci.* 18:130–133.
- Brown, P. M. J., J. Lawson-Handley, O. Nedved, P. De Clercq, and H. E. Roy. 2017. Unravelling the ecology of an invasive ladybird, *Harmonia axyridis*: from populations to communities. *BioControl.* 62: 283–434.
- Camacho-Cervantes, M., A. Ortega-Iturriaga, and E. Del-Val. 2017. From effective biocontrol agent to successful invader: the harlequin ladybird (*Harmonia axyridis*) as an example of good ideas that could go wrong. *PeerJ.* 5: e3296.
- Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage. *Ecol. Lett.* 6: 857–865.
- de Castro-Guedes, C. F., L. M. de Almeida, and M. O. Moura. 2020. Asymmetric intraguild predation of *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) on a native Coccinellidae guild. *Rev. Brasil. De Entomol.* 64: e201969.
- Ceryngier, P., H. E. Roy, and R. L. Poland. 2012. Natural enemies of ladybird beetles. In I. Hodek, H. F. van Emden, and A. Honek (eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley-Blackwell, Chichester, United Kingdom.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Colautti, R. I., and J. A. Lau. 2015. Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Mol. Ecol.* 24: 1999–2017.
- 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.
- Conway, H. E., and T. J. Kring. 2010. Coccinellids associated with the cotton aphid (Homoptera: Aphididae) in Northeast Arkansas cotton. *J. Entomol. Sci.* 45: 129–139.
- Day, W. H., and K. M. Tatman. 2006. Changes in abundance of native and adventive Coccinellidae (Coleoptera) in alfalfa fields, in northern New Jersey (1993–2004) and Delaware (1999–2004). *USA. Entomol. News.* 117: 491–502.
- Didham, R. K., F. Barbero, C. M. Collins, M. L. Forister, C. Hassall, S. R. Leather, L. Packer, M. E. Saunders, and A. J. A. Stewart. 2020. Spotlight on insects: trends, threats and conservation challenges. *Insect Conserv. Divers.* 13: 99–102.
- Diepenbrock, L. M., and D. L. Finke. 2013. Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. *Insect Conserv. Divers.* 6: 671–679.
- Diepenbrock, L. M., K. Fothergill, K. V. Tindall, J. E. Losey, R. R. Smyth, and D. L. Finke. 2016. The influence of exotic lady beetle (Coleoptera: Coccinellidae) establishment on the species composition on the native lady beetle community in Missouri. *Environ. Entomol.* 45: 855–864.
- Glugosch, K. M., S. R. Anderson, J. Braasch, F. A. Cang, and H. D. Gillette. 2015. The devil is in the details: genetic variation in introduced populations and its contributions to invasion. *Mol. Ecol.* 24: 2095–2111.
- Dong, M., D. Zhang, and X. Du. 2011. The relationship between aphids and their natural enemies and the ecological management. *Acta Phyto. Sin.* 38: 327–332.
- Elliott, N., R. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia.* 105: 537–544.
- Elnagdy, S., M. E. Majerus, M. Gardener, and L. J. Lawson Handley. 2013. The direct effects of male killer infection on fitness of ladybird hosts (Coleoptera: Coccinellidae). *J. Evol. Biol.* 26: 1816–1825.

- Evans, E. W. 1991. Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. *Oecologia*. 87: 401–408.
- 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.
- Evans, E. W. 2009. Lady beetles as predators of insects other than Hemiptera. *Biol. Contr.* 51: 255–267.
- Evans, E. W. 2017. Fates of rare species under siege from invasion: Persistence of *Coccinella novemnotata* Herbst in western North America alongside an invasive congener. *Front. Ecol. Evol.* 5: 152.
- Evans, E. W., A. O. Soares, and H. Yasuda. 2011. Invasions by ladybugs, ladybirds, and other predatory beetles. *BioControl*. 56: 597–611.
- Facon, B., L. Crespin, A. Loiseau, E. Lombaert, A. Magro, and A. Estoup. 2011. Can things get worse when an invasive species hybridizes? The harlequin ladybird *Harmonia axyridis* in France as a case study. *Evol. Appl.* 4: 71–88.
- Filatova, I. T. 1974. The parasites of Coccinellidae (Coleoptera) in West Siberia. In Kolomyietz N.G. (ed.), *The fauna and ecology of insects from Siberia*. Publ. House 'Nauka', Siberian Branch, Novosibirsk.
- Finlayson, C. J., K. M. Landry, and A. V. Alyokhin. 2008. Abundance of native and non-native lady beetles (Coleoptera: Coccinellidae) in different habitats in Maine. *Ann. Entomol. Soc. Am.* 101: 1078–1087.
- Flowers, R. W., S. M. Salom, and L. T. Kok. 2006. Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in south-western Virginia. *Agr. Forest Entomol.* 8: 253–262.
- Fonseca, M. M., M. Montserrat, C. Guzmán, I. Torres-Campos, A. Pallini, and A. Janssen. 2017. How to evaluate the potential occurrence of intraguild predation. *Exp. Appl. Acarol.* 72: 103–114.
- Franzmann, B. A. 2002. *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), a predacious ladybird new in Australia. *Austral. J. Entomol.* 41: 375–377.
- Gagnon, A. -E., G. E. Heimpel, and J. Brodeur. 2011. The ubiquity of intraguild predation among predatory arthropods. *PLoS ONE*. 6: e28061. doi:10.1371/journal.pone.0028061
- Gao, C., C. Cui, Y. Gao, G. Zhang, and G. Ren. 2012. Research and analysis of tobacco field aphids and natural enemy occurrence condition in Longjing. *J. Agr. Sci. Yunnan Univ.* 34: 339–343
- Gardiner, M. M., M. E. O'Neal, and D. A. Landis. 2011. Intraguild predation and native lady beetle decline. *PLoS One*. 6: e23576.
- Gardiner, M. M., L. L. Allee, P. M. J. Brown, J. E. Losey, H. E. Roy, and R. R. Smyth. 2012. Lessons from lady beetles: accuracy of monitoring data from US and UK citizen-science programs. *Front. Ecol. Environ.* 10: 471–476.
- Gautier, M., J. Yamaguchi, J. Foucaud, A. Loiseau, A. Ausset, B. Facon, B. Gschloessl, J. Lagnel, E. Loire, H. Parrinello, et al. 2018. The genomic basis of color pattern polymorphism in the harlequin ladybird. *Curr. Biol.* 28: 3296–3302.e7.
- Gegner, T., O. Otti, S. Tragust, and H. Feldhaar. 2015. Do microsporidia function as 'biological weapon' for *Harmonia axyridis* under natural conditions? *Insect Sci.* 22: 353–359.
- Gkounti, V. T., M. Savopoulou-Soultani, and P. G. Milonas. 2014. Intra- and interspecific interactions between *Nephus includens* and *Cryptolaemus montrouzieri*. *J. Appl. Entomol.* 139: 647–653.
- Gordon, R. D. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *J. New York Entomol. Soc.* 93: 1–912.
- Goryacheva, I., and A. Blekhan. 2017. Genetic structure of native and invasive populations of *Harmonia axyridis* Pall. in the light of global invasion. *Russ. J. Gen.* 53: 9–20.
- Goryacheva, I., A. Blekhan, B. Andrianov, and I. Zakharov. 2017. Heritable bacterial endosymbionts in native and invasive populations of *Harmonia axyridis*. *Biol. Invasion.* 19:493–502.
- Greze, A. A., T. Zaviezo, H. E. Roy, P. M. J. Brown, and G. Bizama. 2016. Rapid spread of *Harmonia axyridis* in Chile and its effects on local coccinellid biodiversity. *Divers. Distrib.* 22: 982–994.
- Gu, D., G. Zhang, R. Zhang, and Y. Pang. 2000. Review on fifty years biological control of insect pests in southern China. *Acta Entomol. Sin.* 43:327–335 (In Chinese with English abstract).
- Guo, J., and F. Wan. 2001. Effect of three diets on development and fecundity of the ladybeetles *Harmonia axyridis* and *Propylaea japonica*. *Chin. J. Biol. Contr.* 17:116–120.
- Guo, J., B. Li, and L. Meng. 2016. Effects of intra-guild egg predation on neonate larva development in three ladybird beetles (Coleoptera: Coccinellidae). *Acta Ecol. Sin.* 37: 1826–1831.
- Haelewaters, D., R. F. Comont, E. Y. Zhao, and D. H. Pfister. 2014. *Hesperomyces virescens* (Fungi, Ascomycota, Laboulbeniales) attacking *Harmonia axyridis* (Coleoptera, Coccinellidae) in its native range. *Chin. Sci. Bull.* 59: 528–532.
- Haelewaters, D., S. Y. Zhao, S. Clusella-Trullas, T. E. Cottrell, A. De Kesel, L. Fiedler, A. Herz, H. Hesketh, C. Hui, R. G. Kleespies et al. 2017. Parasites of *Harmonia axyridis*: current research and perspectives. *BioControl*. 62: 355–371.
- Han, B., and Z. Chen. 2001. Searching behaviour of *Coccinella septempunctata* and four varieties of *Leis axyridis* adults on tea aphid honeydew and analysis of honeydew component. *Acta Ecol. Sin.* 20: 491–501.
- Harmon, J. P., E. Stephens, and J. Losey. 2007. The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *J. Insect Conserv.* 11: 85–94.
- Hautier, L., G. San Martin, P. Callier, J. P. de Biseau, and J. C. Gregoire. 2011. Alkaloids provide evidence of intraguild predation on native coccinellids by *Harmonia axyridis* in the field. *Biol. Invasion.* 13: 1805–1814.
- Hautier, L., G. San Martin, J. -P. Jansen, E. Branquart, and J. -C. Gregoire. 2017. Spiny prey, fortunate prey. Dorsal spines are an asset in intraguild interactions among lady beetles. *Fron. Ecol. Evol.* 5: 135.
- He, F., Y. Wang, F. Yan, X. Li, T. Zhao, and D. Pan. 1996. The natural enemy of aphid and its population dynamic state in maize field. *Liaoning Agr. Sci.* 4: 17–21.
- Heimoana, V., L. J. Pilkington, A. Raman, A. Mitchell, H. I. Nicol, A. C. Johnson, and G. M. Gurr. 2017. Integrating spatially explicit molecular and ecological methods to explore the significance of non-crop vegetation to predators of brassica pests. *Agr. Ecosys. Environ.* 239: 12–19.
- Hemphill, J. L., A. Magro, C. Saladin, and A. F. G. Dixon. 2012. Role of intraguild predation in aphidophagous guilds. *J. Appl. Entomol.* 136: 161–170.
- Hentley, W. T., A. J. Vanbergen, A. P. Beckerman, M. N. Brien, R. S. Hails, T. H. Jones, and S. N. Johnson. 2016. Antagonistic interactions between an invasive alien and a native coccinellid species may promote coexistence. *J. Anim. Ecol.* 85: 1087–1097.
- Hesler, L. S., and R. W. Kieckhefer. 2008. Status of exotic and previously common native coccinellids (Coleoptera) in South Dakota landscapes. *J. Kans. Entomol. Soc.* 81: 29–49.
- Hironori, Y., and S. Katsuhiko. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga*. 42: 153–163.
- Hodek, I., and E. W. Evans. 2012. Food relationships, pp. 141–274. In I. Hodek, H. van Emden, and A. Honek (eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley-Blackwell, London, United Kingdom.
- Hodek, I., and J. P. Michaud. 2008. Why is *Coccinella septempunctata* so successful? *Eur. J. Entomol.* 105: 1–12.
- Hodek, I., H. van Emden, and A. Honek. 2012. *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley-Blackwell, London, United Kingdom.
- Honek, A. 2012. Distributions and habitats, pp. 110–140. In I. Hodek, H. van Emden, and A. Honek (eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley-Blackwell, London, United Kingdom.
- Honek, A., and M. Rejmanek. 1982. The communities of adult aphidophagous Coccinellidae (Coleoptera): a multivariate analysis. *Acta Oecol. Oecol. Appl.* 3: 95–104.
- Honek, A., Z. Martinkova, P. Kindlmann, O. M. C. C. Ameixa, and A. F. G. Dixon. 2014. Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe. *Insect Conserv. Diver.* 7: 55–63.
- Honek, A., Z. Martinkova, and A. F. G. Dixon. 2015. Detecting seasonal variation in composition of adult Coccinellidae communities. *Ecol. Entomol.* 40: 543–552.
- Honek, A., Z. Martinkova, A. F. G. Dixon, H. E. Roy, and S. Pekar. 2016. Long-term changes in communities of native coccinellids: population

- fluctuations and the effect of competition from an invasive non-native species. *Insect Conserv. Diver.* 9: 202–209.
- Honek, A., A. F. G. Dixon, A. O. Soares, J. Skuhrovec, and Z. Martinkova. 2017. Spatial and temporal changes in the abundance and composition of ladybird (Coleoptera: Coccinellidae) communities. *Curr. Opin. Insect Sci.* 20: 61–67.
- Honek, A., Z. Martinkova, H. E. Roy, A. F. G. Dixon, J. Skuhrovec, S. Pekár, and M. Brabec. 2019. Differences in the phenology of *Harmonia axyridis* (Coleoptera: Coccinellidae) and native coccinellids in Central Europe. *Environ. Entomol.* 48: 80–87.
- Honek, A., Z. Martinkova, and S. Pekar. 2020a. Threshold aphid population density for starting oviposition in *Harmonia axyridis*. *BioControl.* 65: 425–432.
- Honek, A., P. M. J. Brown, Z. Martinkova, J. Skuhrovec, M. Brabec, G. Burgio, E. W. Evans, M. Fournier, A. A. Grez, J. Kulfan, et al. 2020b. Factors determining variation in color morph frequencies in invasive *Harmonia axyridis* populations. *Biol. Invasion.* 22: 2049–2062.
- Howe, A. G., H. P. Ravn, C. B. Pipper, and A. Aebi. 2016. Potential for exploitative competition, not intraguild predation, between invasive harlequin ladybirds and flowerbugs in urban parks. *Biol. Invasion.* 18: 517–532.
- Huang, J., Xu, L.-Y., and J.-W. Xu. 1998. Commercialization of natural enemy products abroad and introduction of *Delphastus catalinae* (LeConte) (Coleoptera: Coccinellidae) into China. *Entomol. J. East China.* 7: 101–104.
- Jonsson, M., R. Kaartinen, and C. S. Straub. 2017. Relationships between natural enemy diversity and biological control. *Curr. Opin. Insect Sci.* 20: 1–6.
- Kajita, Y., and E. W. Evans. 2010a. Alfalfa fields promote high reproductive rate of an invasive predatory lady beetle. *Biol. Invasion.* 12: 2293–2302.
- Kajita, Y., and E. W. Evans. 2010b. Relationships of body size, fecundity, and invasion success among predatory lady beetles (Coleoptera: Coccinellidae) inhabiting alfalfa fields. *Ann. Entomol. Soc. Am.* 103: 750–756.
- 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. *Jpn J. App. Entomol. Zool.* 35: 473–479.
- Kajita, Y., E. M. O'Neill, Y. Zheng, J. J. Obrycki, and D. W. Weisrock. 2012. A population genetic signature of human releases in an invasive lady beetle. *Mol. Ecol.* 21: 5473–5483.
- Katsanis, A., D. Babendreier, W. Nentwig, and M. Kenis. 2013. Intraguild predation between the invasive ladybird *Harmonia axyridis* and non-target European coccinellid species. *BioControl.* 58: 73–83.
- Kenis, M., T. Adriaens, P. M. J. Brown, A. Katsanis, G. San Martin, E. Branquart, D. Maes, R. Eschen, R. Zindel, J. Van Vlaenderen, et al. 2017. Assessing the ecological risk posed by a recently established invasive alien predator: *Harmonia axyridis* as a case study. *BioControl.* 62: 341–354.
- Kindlmann, P., and K. Houdkova. 2006. Intraguild predation: fiction or reality? *Popul. Ecol.* 48: 317–322.
- Kindlmann, P., A. F. G. Dixon, and J. P. Michaud. 2010. Aphid biodiversity under environmental change: patterns and processes. Springer, New York.
- Kindlmann, P., O. M. C. C. Ameixa, and A. F. G. Dixon. 2011. Ecological effects of invasive alien species on native communities, with particular emphasis on the interactions between aphids and ladybirds. *BioControl.* 56: 469–476.
- Kindlmann, P., A. Honek, and Z. Martinkova. 2017. Spreading of alien species and diversity of communities. *BioControl.* 62: 397–407.
- van Kleunen, M., W. Dawson, D. Schlaepfer, J. M. Jeschke, and M. Fischer. 2010. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecol. Lett.* 13: 947–958.
- van Klink, R., D. E. Bowler, K. B. Gongalsky, A. B. Swengel, A. Gentile, and J. M. Chase. 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science.* 368: 417–420.
- Koch, R. L., and A. C. Costamagna. 2017. Reaping benefits from an invasive species: role of *Harmonia axyridis* in natural biological control of *Aphis glycines* in North America. *BioControl.* 62: 331–340.
- Koch, R. L., and T. L. Galvan. 2008. Bad side of a good beetle: the North American experience with *Harmonia axyridis*. *BioControl.* 53: 23–35.
- Koyama, S., and M. E. N. Majerus. 2008. Interactions between the parasitoid wasp *Dinocampus coccinellae* and two species of coccinellid from Japan and Britain. *BioControl.* 53: 253–264.
- Kring, T. J., and F. E. Gilstrap. 1986. Beneficial role of corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Homoptera: Aphididae), in maintaining *Hippodamia* spp. (Coleoptera: Coccinellidae) in grain sorghum. *Crop Prot.* 5: 125–128.
- Kuznetsov, V. N. 1997. Lady beetles of the Russian Far East. Center for Systematic Entomology. Sandhill Crane Press, Gainesville, FL, USA.
- Lamb, R. J., J. A. Bannerman, and A. C. Costamagna. 2019. Stability of native and exotic lady beetle populations in a diverse landscape. *Ecosphere.* 10: e02630.
- Lamb, R. J., J. A. Bannerman, and A. C. Costamagna. 2020. Interactions between exotic and native lady beetle species stabilize community abundance. *Oecologia.* 193: 701–711.
- Lawson Handley, L.-J., A. Estoup, D. M. Evans, C. E. Thomas, E. Lombaert, B. Facon, A. Aebi, and H. E. Roy. 2011. Ecological genetics of invasive alien species. *BioControl.* 56: 409–428.
- Lenhart, P. A., K. A. Jackson, and J. A. White. 2018. Heritable variation in prey defence provides refuge for subdominant predators. *Proc. R. Soc. B.* 285: 20180523.
- Li, L.-Y. 1993. The research and application prospects of *Cryptolaemus montrouzieri* in China. *Nat. Enemies Insect.* 15: 142–152 (In Chinese with English abstract).
- Li, H. R. 2020. A comparative study of genetic and endosymbiotic diversity between *Harmonia axyridis* populations in its native and invaded ranges. Ph.D. dissertation, Nanjing Agricultural University, Nanjing, China. (In Chinese with English abstract)
- Liang, X. 2017. Population dynamics and influencing factors of *Coccinella septempunctata* and *Harmonia axyridis* in the wheat fields. Master's Degree thesis, Shandong Agricultural University, Shandong, China (In Chinese with English summary).
- Li, C., W. Wu, L. Zhu, Q. Zhang, and X. Liu. 2011. Effects of wheat planted adjacent to rape on the major pests and their natural enemies in wheat field. *Chin. J. Appl. Ecol.* 22: 3371–3376. (In Chinese with English abstract)
- Liu, J., and D. He. 2008. Study on inter species competition between *Coccinella septempunctata* and *Harmonia axyridis* against *Myzus persicae*. *China Plant Prot.* 28: 9–12. (In Chinese with English abstract)
- Liu, J., W. Xu, Q. Wang, and K. Zhao. 2012. Insect predators in northeast China and their impacts on *Aphis glycines*. *Can. Entomol.* 144: 745–755.
- Lombaert, E., T. Guillemaud, J. M. Cornuet, T. Malausa, B. Facon, and A. Estoup. 2010. Bridgehead effect in the worldwide invasion of the bio-control harlequin ladybird. *Plos One.* 5: e9743.
- Lombaert, E., A. Estoup, B. Facon, B. Joubard, J. C. Grégoire, A. Jannin, A. Blin, and T. Guillemaud. 2014. Rapid increase in dispersal during range expansion in the invasive ladybird *Harmonia axyridis*. *J. Evol. Biol.* 27: 508–517.
- Lövei, G. L., M. Sárospataki, and Z. Radwan. 1991. Structure of ladybird (Coleoptera: Coccinellidae) assemblages in apple: changes through developmental stages. *Environ. Entomol.* 20: 1301–1308.
- Lu, Z., P. Shi, G. V. P. Reddy, L. Li, X. Men, and F. Ge. 2015. Nonparametric estimation of interspecific spatio-temporal niche separation between two lady beetles (Coleoptera: Coccinellidae) in Bt-cotton fields. *Ann. Entomol. Soc. Am.* 108: 807–813.
- Lucas, E. 2005. Intraguild predation among aphidophagous predators. *Eur. J. Entomol.* 102: 351–364.
- Lucas, E. 2012. Intraguild Interactions. pp. 343–374. In I. Hodek, H. van Emden, and A. Honek (eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley-Blackwell, London, United Kingdom.
- Lucas, E., G. Labrie, C. Vincent, and J. Kovach. 2007. The multicoloured Asian ladybird beetle: beneficial or nuisance organism? pp. 38–52. In C. Vincent, M. Goettel, and G. Lazarovits (eds.), *Biological control: a global perspective*. CAB International, UK.
- Lundgren, J. G., and D. C. Weber. 2009. Trophic ecology of the Coccinellidae. *Biol. Contr.* 51: 199–335.
- Majerus, T. M. O., M. E. N. Majerus, B. Knowles, J. Wheeler, D. Bertrand, V. N. Kuznetsov, H. Ueno, and G. D. D. Hurst. 1998. Extreme variation in the prevalence of inherited male-killing microorganisms between three populations of *Harmonia axyridis* (Coleoptera: Coccinellidae). *Heredity.* 81: 683–691.
- Masetti, A., S. Magagnoli, F. Lami, A. Lanzoni, and G. Burgio. 2018. Long term changes in the communities of native ladybirds in Northern Italy:

- impact of the invasive species *Harmonia axyridis* (Pallas). *BioControl*. 63: 665–675.
- Meisner, M., J. P. Harmon, C. T. Harvey, and A. R. Ives. 2011. Intraguild predation on the parasitoid *Aphidius ervi* by the generalist predator *Harmonia axyridis*: the threat and its avoidance. *Entomol. Appl. Exp.* 138: 193–201.
- 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.
- Michaud, J. P. 2012. Coccinellids in biological control, pp. 488–519. In I. Hodek, H. F. van Emden, and A. Honek (eds.), *Ecology and behaviour of the ladybird beetles* (Coccinellidae). Wiley-Blackwell, Chichester, United Kingdom.
- Michaud, J. P., and J. D. Harwood. 2012. Quantifying the impact of coccinellids on their prey, pp. 465–487. In I. Hodek, H. F. van Emden, and A. Honek (eds.), *Ecology and behaviour of the ladybird beetles* (Coccinellidae). Wiley-Blackwell, Chichester, United Kingdom.
- Mirande, L., N. Desneux, M. Haramboure, and M. I. Schneider. 2015. Intraguild predation between an exotic and a native coccinellid in Argentina: the role of prey density. *J. Pest Sci.* 88:155–162.
- Moser, S. E., and J. J. Obrycki. 2009. Competition and intraguild predation among three species of Coccinellids (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* 102: 419–425.
- Mukwevho, V. O., J. S. Pryke, and F. Roets. 2017. Habitat preferences of the invasive harlequin ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae) in the Western Cape Province, South Africa. *Afr. Entomol.* 25: 86–97.
- Nedved, O. 1999. Host complexes of predaceous ladybeetles (Col., Coccinellidae). *J. Appl. Entomol.* 123: 73–76.
- Nijijima, K., M. Matsuka, and I. Okada. 1986. Artificial diets for an aphidophagous coccinellid, *Harmonia axyridis*, and its nutrition, pp. 37–50. In I. Hodek (ed.), *Ecology of aphidophaga*. Academia, Prague and W. Junk, Dordrecht.
- Obrycki, J. J., and T. J. Kring. 1998. Predaceous Coccinellidae in biological control. *Annu. Rev. Entomol.* 43: 295–321.
- Obrycki, J. J., N. C. Elliott, and K. L. Giles. 2000. Coccinellid introductions: potential for and evaluation of non-target effects, pp. 127–145. In P. A. Follett and J. J. Duan (eds.), *Nontarget effects of biological control*. Kluwer Academic Publishers, Dordrecht.
- Obrycki, J. J., T. J. Kring, J. D. Harwood, and R. J. O'Neil. 2009. Aphidophagy by Coccinellidae: application of biological control in agroecosystems. *Biol. Contr.* 51: 244–254.
- Orlova-Bienkowskaja, M. J., A. S. Ukrainsky, and P. M. J. Brown. 2015. *Harmonia axyridis* (Coleoptera: Coccinellidae) in Asia: a re-examination of the native range and invasion to southeastern Kazakhstan and Kyrgyzstan. *Biol. Invasion.* 17:1941–1948.
- Orlova-Bienkowskaja, M. J., S. E. Spiridonov, N. N. Butorina, and A. O. Bieńkowski. 2018. Coinvasion by the ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae) and its parasites, *Hesperomyces virescens* (Ascomycota: Laboulbeniales) and *Parasitylenchus bifurcatus* (Nematoda: Tylenchida, Allantonematidae), in the Caucasus. *PLoS One*. 13: e0202841.
- Ortiz-Martinez, S., K. Staudacher, V. Baumgartner, M. Traugott, and B. Lavandero. 2020. Intraguild predation is independent of landscape context and does not affect the temporal dynamics of aphids in cereal fields. *J. Pest Sci.* 93: 235–249.
- Osawa, N. 1992. A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera Coccinellidae) in relation to the aphid abundance. *Jpn J. Entomol.* 60: 575–579.
- Osawa, N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae): life tables and key factor analysis. *Res. Popul. Ecol.* 35: 335–348.
- Osawa, N. 2010. The ecology of *Harmonia axyridis* in its native range. *IOBC/WPRS Bull* 58: 69–73.
- Osawa, N. 2011. Ecology of *Harmonia axyridis* in natural habitats within its native range. *BioControl*. 56: 613–621.
- Ovchinnikova, A. N., N. A. Belyakova, A. A. Ovchinnikova, and S. Y. Reznik. 2019. Factors determining larval cannibalistic behavior in invasive and native populations of the multicolored Asian ladybird, *Harmonia axyridis*. *Entomol. Gen.* 38: 243–254.
- Pell, J. K., J. Baverstock, H. E. Roy, R. L. Ware, and M. E. N. Majerus. 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. *BioControl*. 53: 147–168.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297–330.
- Poutsma, J., A. J. M. Loomans, B. Aukema, and T. Heijerman. 2008. Predicting the potential geographical range distribution of the harlequin ladybird, *Harmonia axyridis*, using the CLIMEX model. *BioControl*. 53: 103–125.
- Powell, W., and J. K. Pell. 2007. Biological control, pp. 469–513. In H. F. van Emden, and R. Harrington (eds.), *Aphids as crop pests*. CAB International, Cambridge, MA.
- Raak-van den Berg, C. L., H. J. De Lange, and J. C. Van Lenteren. 2012. Intraguild predation behaviour of ladybirds in semi-field experiments explains invasion success of *Harmonia axyridis*. *PLoS One*. 7: e40681.
- Raak-van den Berg, C. L., L. Hemerik, W. van der Werf, P. W. de Jong, and J. C. van Lenteren. 2017. Life history of the harlequin ladybird, *Harmonia axyridis*: a global meta-analysis. *BioControl* 62: 283–296.
- Raak-van den Berg, C. L., P. W. Jong, G. Gort, B. F. J. Manly, and J. C. Lenteren. 2018. Life histories of an invasive and native ladybird under field experimental conditions in a temperate climate. *Entomol. Exp. Appl.* 166: 151–161.
- Ragsdale, D. W., D. A. Landis, J. Brodeur, G. E. Heimpel, and N. Desneux. 2011. Ecology and management of the soybean aphid in North America. *Annu. Rev. Entomol.* 56: 375–399.
- Rasekh, A., and N. Osawa. 2020. Direct and indirect effect of cannibalism and intraguild predation in the two sibling *Harmonia* ladybird beetles. *Ecol. Evol.* 10: 5899–5912.
- Rebolledo, R., J. Sheriff, L. Parra, and A. Aguilera. 2009. Life, seasonal cycles, and population fluctuation of *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), in the central plain of La Araucania region, Chile. *Chil. J. Agric. Res.* 69: 292–298.
- Reitz, S. R., and J. T. Trumble. 2002. Competitive displacement among insects and arachnids. *Annu. Rev. Entomol.* 47: 435–465.
- Ren, S., X. Wang, H. Pang, Z. Peng, and T. Zeng. 2009. Colored pictorial handbook of ladybird beetles in China. Science Press, Beijing, China.
- Reznik, S. Ya., M. Yu. Dolgovskaya, A. N. Ovchinnikov, and N. A. Belyakova. 2015. Weak photoperiodic response facilitates the biological invasion of the harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *J. Appl. Entomol.* 139: 241–249.
- Riddick, E. W. 2017. Spotlight on the positive effects of the ladybird *Harmonia axyridis* on agriculture. *BioControl*. 62: 319–330.
- Riddick, E. W., T. E. Cottrell, and K. A. Kidd. 2009. Natural enemies of the Coccinellidae: parasites, pathogens, and parasitoids. *Biol. Contr.* 51: 306–312.
- Rondoni, G., K. J. Athey, J. D. Harwood, E. Conti, C. Ricci, and J. J. Obrycki. 2015. Development and application of molecular gut-content analysis to detect aphid and coccinellid predation by *Harmonia axyridis* (Coleoptera: Coccinellidae) in Italy. *Insect Sci.* 22: 719–730.
- Rondoni, G., F. Ielo, C. Ricci, and E. Conti. 2017. Behavioural and physiological responses to prey-related cues reflect higher competitiveness of invasive vs. native ladybirds. *Sci. Rep.* 7: 3716.
- Rondoni, G., S. Fenjan, V. Bertoldi, F. Ielo, K. Djelouah, C. Moretti, R. Buonauro, C. Ricci, and E. Conti. 2018. Molecular detection of field predation among larvae of two ladybird beetles is partially predicted from laboratory experiments. *Sci. Rep.* 8: 2594.
- Rondoni, G., I. Borges, J. Collatz, E. Conti, A. Costamagna, F. Dumont, E. W. Evans, A. A. Grez, A. G. Howe, E. Lucas, et al. 2020. Exotic ladybirds for biological control of herbivorous insects—a review. Special Issue: 6th Inter. Entomophagous Insects Conf. *Entomol. Exp. Appl.* doi:10.1111/eea.12963.
- Roy, H. E., and E. Wajnberg. 2008. From biological control to invasion: the ladybird *Harmonia axyridis* as a model species. *BioControl*. 53: 1–287.

- Roy, H. E., T. Adriaens, N. J. B. Isaac, M. Kenis, T. Onkelinx, G. San Martin, P. M. J. Brown, L. Hautier, R. Poland, D. B. Roy, et al. 2012. Invasive alien predator causes rapid declines of native European ladybirds. *Diver. Distrib.* 18: 717–725.
- Roy, H. E., P. M. J. Brown, T. Adriaens, N. Berkvens, I. Borges, S. Clusella-Trullas, R. F. Comont, P. De Clercq, R. Eschen, A. Estoup, et al. 2016. The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. *Biol. Invasion* 18: 997–1044.
- Royer, T. A., K. L. Giles, M. M. Lebusa, and M. E. Payton. 2008. Preference and suitability of greenbug, *Schizaphis graminum* (Hemiptera: Aphididae) mummies parasitized by *Lysiphlebus testaceipes* (Hymenoptera: Aphididae) as food for *Coccinella septempunctata* and *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biol. Contr.* 47: 82–88.
- Sakuratani, Y. 1994. New record of *Adalia bipunctata* (Linnaeus) (Coleoptera: Coccinellidae) from Japan. *J. Appl. Entomol. Zool.* 62: 627–628.
- Sakuratani, Y., Y. Matsumoto, M. Oka, T. Kubo, A. Fuji, M. Uotani, and T. Teraguchi. 2000. Life history of *Adalia bipunctata* (Coleoptera: Coccinellidae) in Japan. *Eur. J. Entomol.* 97: 555–558.
- Salas Gervasio, N. G., M. Pérez-Hedo, M. G. Luna, and A. Urbaneja. 2017. Intraguild predation and competitive displacement between *Nesidiocoris tenuis* and *Dicyphus maroccanus*, two biological control agents in tomato pests. *Insect Sci.* 24: 809–817.
- Sanchez-Bayo, F., and K. A. G. Wyckhuys. 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232: 8–27.
- Sato, S., H. Yasuda, and A. F. G. Dixon. 2003. Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecol. Entomol.* 28: 628–633.
- Sato, S., K. Shinya, H. Yasuda, P. Kindlmann, and A. F. G. Dixon. 2009. Effects of intra and interspecific interactions on the survival of two predatory ladybirds (Coleoptera: Coccinellidae) in relation to prey abundance. *Appl. Entomol. Zool.* 44: 215–221.
- Schandler, H., A. Ferran, and V. Garcia. 1988. L'élevage de deux coccinelles *Harmonia axyridis* et *Semidalia undecimnotata* à l'aide d'oeufs d'*Anagasta kuehniella* tués aux rayons ultraviolets. *Entomol. Exp. Appl.* 49: 235–244.
- Sethuraman, A., F. J. Janzen, M. A. Rubio, Y. Vasquez, and J. J. Obrycki. 2018. Demographic histories of 3 predatory lady beetles reveal complex patterns of diversity and population size change in the United States. *Insect Sci.* 25: 1065–1079.
- Sethuraman, A., F. J. Janzen, D. W. Weisrock, and J. J. Obrycki. 2020. Insights from population genomics to enhance and sustain biological control of insect pests. *Insects* 11: 462.
- Shao, T., X. Liu, and K. Wang. 2014. Occurrence dynamics of *Longiunguis sacchari* and several natural enemies in sorghum field. *J. Beihua Univ.* 15: 258–260.
- Sloggett, J. J. 2012. *Harmonia axyridis* invasions: deducing evolutionary causes and consequences. *Entomol. Sci.* 15: 261–273.
- Smith, C. A., and M. M. Gardiner. 2013. Biodiversity loss following the introduction of exotic competitors: does intraguild predation explain the decline of native lady beetles? *PLoS One* 8: e84448.
- Snyder, W. E. 2009. Coccinellids in diverse communities: which niche fits? *Biol. Contr.* 51: 323–335.
- Snyder, W. E., and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. *Annu. Rev. Ecol. Evol. Syst.* 37: 95–122.
- Snyder, W. E., and J. M. Tylianakis. 2012. The ecology of biodiversity–biocontrol relationships, pp. 23–40. In G. M. Gurr, S. D. Wratten, W. E. Snyder, and D. M. Y. Read (eds.), *Biodiversity and insect pests: key issues for sustainable management*. John Wiley & Sons Publ, Chichester, UK.
- Soares, A. O., A. Honek, Z. Martinkova, P. M. J. Brown, and I. Borges. 2018. Can native geographical range, dispersal ability and development rates predict the successful establishment of alien ladybird (Coleoptera: Coccinellidae) species in Europe? *Front. Ecol. Evol.* 6: 57.
- Song, H. 2017. Behavioral ecology of gregarious parasitoids (Hymenoptera: Eulophidae) attacking the ladybird *Coccinella septempunctata*. Ph.D dissertation, Nanjing Agricultural University, Nanjing, China (In Chinese with English abstract).
- Song, H., L. Meng, and B. Li. 2017. Fitness consequences of body-size-dependent parasitism in a gregarious parasitoid attacking the 7-spot ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Biol. Contr.* 113: 73–79.
- Song, H. T., M. H. Fei, B. P. Li, C. D. Zhu, and H. X. Cao. 2020. A new species of *Oomyzus* Rondani (Hymenoptera, Eulophidae) reared from the pupae of *Coccinella septempunctata* (Coleoptera, Coccinellidae) in China. *Zookeys* 953: 49–60.
- Staines, C. L., M. J. Rothschild, and R. B. Trumble. 1990. A survey of the Coccinellidae (Coleoptera) associated with nursery stock in Maryland. *Proc. Entomol. Soc. Wash.* 92: 310–313.
- Straub, C. S., and W. E. Snyder. 2008. Increasing enemy biodiversity strengthens herbivore suppression on two plant species. *Ecology* 89: 1605–1615.
- Straub, C. S., D. L. Finke, and W. E. Snyder. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biol. Contr.* 45: 225–237.
- Tayeh, A., A. Estoup, E. Lombaert, T. Guillemaud, N. Kirichenko, L. Lawson-Handley, P. De Clercq, and B. Facon. 2014. Cannibalism in invasive, native and biocontrol populations of the harlequin ladybird. *BMC Evol. Biol.* 14: 15.
- Tedders, W. L., and P. W. Schaefer. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. *Entomol. News* 105: 228–243.
- The Lost Ladybug Project. www.lostladybug.org. Accessed on 25 September 2020.
- Thomas. 2013. Predation of native coccinellids by the invasive alien *Harmonia axyridis* (Coleoptera: Coccinellidae): detection in Britain by PCR-based gut analysis. *Insect Conser. Diver.* 6: 20–27.
- Toda, Y., and Y. Sakuratani. 2006. Expansion of the geographical distribution of an exotic ladybird beetle, *Adalia bipunctata* (Coleoptera: Coccinellidae), and its interspecific relationships with native ladybird beetles in Japan. *Ecol. Res.* 21: 292–300.
- Tsushima, Y., K. Nakamura, Y. Tagami, and K. Miura. 2015. Mating rates and the prevalence of male-killing *Spiroplasma* in *Harmonia axyridis* (Coleoptera: Coccinellidae). *Entomol. Sci.* 18: 217–220.
- Tumminello, G., T. A. Ugine, and J. E. Losey. 2015. Intraguild interactions of native and introduced coccinellids: the decline of a flagship species. *Environ. Entomol.* 44: 64–72.
- Turnock, W. J., I. L. Wise, and F. O. Matheson. 2003. Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *Can. Entomol.* 135: 391–404.
- Ugine, T. A., S. B. Krasnoff, R. J. Grebenok, S. T. Behmer, and J. E. Losey. 2019. Prey nutrient content creates omnivores out of predators. *Ecol. Lett.* 22: 275–283.
- Volkl, W., M. Mackauer, J. K. Pell, and J. Brodeur. 2007. Predators, parasitoids, and pathogens, pp. 187–233. In H. F. van Emden and R. Harrington (eds.), *Aphids as crop pests*. CAB Inter, Cambridge, MA.
- Wagner, D. L. 2020. Insect declines in the anthropocene. *Annu. Rev. Entomol.* 65: 457–480.
- Wang, R., Y. Cao, and Z. Wu. 2012. Influence of shelterbelt on population distribution for ladybug. *Protect. Forest Sci. Tech.* 1: 53–56.
- Wang, X., F. Ouyang, and Y. Liu. 2013. Effects of farmland landscape patterns on the population dynamics of two lady beetles. *Chin. J. Appl. Entomol.* 50: 903–911.
- Ware, R. L., and M. E. N. Majerus. 2008. Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*. *BioControl* 53: 169–188.
- Ware, R. L., B. Yguel, and M. Majerus. 2009. Effects of competition, cannibalism and intra-guild predation on larval development of the European coccinellid *Adalia bipunctata* and the invasive species *Harmonia axyridis*. *Ecol. Entomol.* 34: 12–19.
- Weinert, L. A., M. C. Tinsley, M. Temperley, and F. M. Jiggins. 2007. Are we underestimating the diversity and incidence of insect bacterial symbionts? A case study in ladybird beetles. *Biol. Lett.* 3: 678–681.
- Wells, P. M., J. Baverstock, S. J. Clark, F. M. Jiggins, H. E. Roy, and J. K. Pell. 2017. Determining the effects of life stage, shared prey density and host plant on intraguild predation of a native lacewing (*Chrysoperla carnea*) by an invasive coccinellid (*Harmonia axyridis*). *BioControl* 62: 373–384.

- Wu, W., D. Liu, P. Zhang, and Z. Zhang. 2011. Community structure and diversity ladybugs in Baihualing of Gaoligong Mountain. I. J. Anhui Agri. Sci. 39: 19151–19153 (In Chinese with English abstract).
- Yang, F., Q. Wang, D. Wang, B. Xu, J. Xu, Y. Lu, and J. D. Harwood. 2017. Intraguild predation among three common coccinellids (Coleoptera: Coccinellidae) in China: detection using DNA-based gut-content analysis. Environ. Entomol. 46: 1–10.
- Yasuda, H., and T. Kimura. 2001. Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. Entomol. Exp. Appl. 89: 17–25.
- Yasuda, H., and Y. Shinya. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga. 42: 153–163.
- Zakharov, I. A., N. S. Zinkevich, E. V. Shaikovich, L. V. Vysotskaya, C. M. Dorzhu, and M. E. N. Majerus. 1999. Sex ratio and male killing in Siberian populations of *Harmonia axyridis* Pall. Russ. J. Gen. 35: 653–657.
- Zaviezo, T., A. O. Soares, and A. A. Grez. 2019. Interspecific exploitative competition between *Harmonia axyridis* and other coccinellids is stronger than intraspecific competition. Biol. Control. 131: 62–68.
- Zhao, G., Z. Lian, and J. Zhao. 2020. A survey of beneficial lady beetles in fruit orchards at Pudong, Shanghai city. Shanghai Agri. Tech. (1) 125–126 (In Chinese).
- Zhu, S., A. Fan, J. Song, and X. Hong. 2002. Investigation on populations of ladybirds and spiders in cotton field and their functions. Plant Prot. Tech. Ext. 23: 5–7, 32 (In Chinese with English abstract).