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

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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, Rebollo 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 (Obycky 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 Obycky 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 intraspecific differences in these species. We also discuss experimental
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; Haitier 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, Haitier 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 intraguild prey, and given the ephemeral nature of aphid infestations, such control rarely occurs in these predator–aphid prey systems. Similarly, based on modeling and
| Goal/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 Ha 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 Ha and A2 adults on lime trees. Change in coccinellid community structure. Strong indication that declines in A2 caused by Ha. Proportion of native spp. declined from 99.8 to 31%. Collected 21 native and 1 non-native spp.; A2, C5, and P14 decreased; declines prior to Ha arrival; A10, Ca14 increasing prior to Ha but then declined. Shannon diversity for native species similar over 40 yr; Several factors (Ha, climate change, land use patterns) influence native species composition and long-term population fluctuations | Brown and Roy 2018 |
| Assess native species abundance and community composition on deciduous trees before and after Ha arrival | 1976–1986, 2002–2006 vs. 2011–2014 | Czech Republic | Before, just before, and after Ha arrival; May–July sweep net samples of adults; deciduous trees; 1–2 samples/mo | Ha 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. 2016 |
| Hypothesis: Long-term reductions in native species abundance correlated with high abundance and wide distribution of Ha | 1976–1986 vs. 2010–2016 | Czech Republic | Cereal, herbaceous habitats and trees; fortnightly sweep net samples of adults, L3, L4, trees sampled Apr.–Nov.; cereals and herbaceous plants >30 cm until senescence | Documented 21 spp.; seasonal trends similar over 5 yr; A10 most abundant sp. in May–June; Ha most abundant in late summer; Shannon diversity decreased during summer; 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. 2015 |
| 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. | | |
| Assess effects of land use changes and Ha on coccinellid communities | 1976–1983 vs. 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 Ha | In 2015–2016, Ha 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 Ha in herbaceous habitats -little effect on native spp. | Masetti et al. 2018 |
| 1) evaluate Ha impact on lady beetle communities; 2) describe changes over 20 yr in community structure; 3) document native species decline after Ha arrival | 1995–1996 & 2015–2016 | N Italy | Before vs. after Ha 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) | | |
| **North America**          |              |          |                                                      |                         |           |
| Document effects of C7 on common native coccinellid species | 1983–2001 & 1989–2001, 1999–2001 | 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. tru, 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 25 plants in potato plots | Density of lady beetle populations and relative abundance of individual lady beetle species varied yearly; before 1980 native C. tru & H13 very abundant; C7 6% in 1980, 100% in 1994; C. tru and H13 declined but persisted; P14 arrives in 1993, Ha 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 5 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—increased in number of native species, primarily Co. mac. Mentions reduction in pea aphid densities, but data not collected | Day and Tatman 2006 |
| Study period | Location | Study period | Location | Study period | Location |
|--------------|----------|--------------|----------|--------------|----------|
| 1988–2015 Utah, USA | 1992–2001 Utah, USA | 1991–1997 Utah, USA |
| 5 nonconsecutive years | 5 nonconsecutive years | 5 nonconsecutive years |
| 1989–1994 vs. 1994–1998 Michigan, USA | 1986–1988 Maryland, USA | 1991–1997 Utah, USA |
| 2001–2006 S. Dakota, USA | 1991–1997 Utah, USA | 1991–1997 Utah, USA |
| 1973–1985 vs. 1988–1992 S. Dakota, USA | 1991–1997 Utah, USA | 1991–1997 Utah, USA |
| 118 yr Missouri, USA | 1989–1994 vs. 1994–1998 Michigan, USA | 1991–1997 Utah, USA |
| 1986–1988 Maryland, USA | 1991–1997 Utah, USA | 1991–1997 Utah, USA |
| 2001–2006 S. Dakota, USA | 1991–1997 Utah, USA | 1991–1997 Utah, USA |
| 1973–1985 vs. 1988–1992 S. Dakota, USA | 1991–1997 Utah, USA | 1991–1997 Utah, USA |
| 118 yr Missouri, USA | 1989–1994 vs. 1994–1998 Michigan, USA | 1991–1997 Utah, USA |

| Goals/hypothesis/objectives | Habitat, sampling methods, and life stages collected | Results and conclusions | Reference |
|----------------------------|---------------------------------------------------|-------------------------|-----------|
| Quantify populations of C9 after C7 establishment in N American intermountain western region | 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. | 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 | 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. sm, 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 | 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 | 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 |
| Analyze population dynamics, species diversity; model potential of lady beetle community to suppress herbivores | 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 |
| Characterize populations of native and non-native coccinellid spp.; identify refuge habitats of native species | 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 | 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 | 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

| Habitat, sampling methods, and life stages | Results and conclusions | Reference |
|------------------------------------------|-------------------------|-----------|
| Goals/hypothesis/objectives               |                         |           |
| Study period Location                     |                         |           |
| 1997–1998 vs. Florida, USA               | Before vs. after Ha arrival; Visual counts of adults on trees; 19 samples; 5 counties in Florida | Goz et al. 2016 |
| 2000–2001                                | Relative abundance of Ha increased; relative abundance of C. septempunctata decreased |           |
| 2010–2014 Chile                          | Sampled adults using 5 sticky cards/field; 10–18 native and 8 non-native spp.; non-native more abundant; 2012: Ha most common sp. Decrease in sp. richness and diversity with Ha increase. | Grez et al. 2016 |
| 2016 Commercial fields; one sample period in spring | Document invasion of Ha in Chile; assess changes in native species in alfalfa. |           |
| Long-term gradual declines in several coccinellid species also occurred 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). |           |

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 | 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\(^a\) survived more than C7; Ha L4 with highest IGP and cannibalism; Ha > C7 IGP asymmetry | Hironori and Katsuhiro 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, Oenopia conglobata (native spp.) | Linden trees, N. Italy | Molecular gut analysis of larvae | Results: 1.5% tested larvae had A2 egg DNA; 5% O. conglobata 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 Adalia spp, Calvia spp and P-14 found | Hautier et al. 2011 |
| Ha vs. A2, A10 | Linden trees, Eastern England | Molecular gut analysis of larval for Adalia 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 |

\(^a\)A2, Adalia bipunctata; A10, Adalia decempunctata; Ca14, Calvia quatuordecimguttata; Chcar, Chrysopa carnea; Cmac, Coleomegilla maculata; C7, Coccinella septempunctata; Ebal, Episyrphus balteatus; Er Eriopis chilensis Ha, Harmonia axyridis; Hvar, Hippodamia variegata; P14, Propylea quatuordecimpunctata.

\(^b\)L3, 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, Honke 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 biodiversity, but if the displacement is one-for-one, biodiversity is unchanged at a local scale. Authors often conclude that this is a reduction in biodiversity, but frequently do not state 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; Bahli 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 Tylianakis 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 Virginia apple orchards, H. axyridis has negatively interacted with C. septempunctata, but provided higher levels of Aphis spiraecola 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 pseudococcus (Homoptera: 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, Orlov-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 species with a long history of coexistence within its native range. With a third species 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 | Methods                                      | Reference        |
|-----------------------------------------|------------------|------------------------------------------------------------------|---------------------------------------------|-------------------------------------------|------------------|
| China                                   |                  |                                                                 |                                             |                                           |                  |
| Shenyang city, Liaoning Province        | Maize            | *H. axyridis, P. japonica, Chrysopa sinica, Ch. septempunctata + 3–5 other spp.* | 1980: Chse (35.8%) > Chs (30.7%) > Ha (15.4) > Pj (6.1) <br>1981: Ha (53.5%) > Pj (8.9%) > Chs (2.9%) > Chse (2%) <br>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            | *H. axyridis, P. japonica*                                        | Pj (67%) > Ha (33%)                           | 1-yr survey; relative abundance estimated from figures. | Wang et al. 2013  |
| Langfang city, Hebei Province           | Cotton           | *H. axyridis, P. japonica*                                        | Pj (53%) > Ha (47%)                           | 1-yr survey; relative abundance estimated from figures. | Wang et al. 2013  |
| Harbin city, Heilongjiang Province      | Sorghum          | *H. axyridis, P. japonica, Ch. sinica.*                           | 2012: Chs (37.5%) > Ha (35.0%) > Pj (27.3%) <br>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           | *H. axyridis, C. septempunctata, P. japonica,* 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           | *H. axyridis, C. septempunctata*                                  | Whereas the two lady beetles were similar in densities during the first 7 yr but from then C7 was obviously more abundant than Ha. | 26-yr (1991–2016) data; yearly totals | Liang 2017       |
| Langfang city, Hebei Province           | Wheat            | *P. japonica, C. septempunctata, Ch. septempunctata + 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          | *P. japonica, C. septempunctata + 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 | *P. japonica, H. axyridis + 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   | *H. axyridis, C. septempunctata + 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   | *P. japonica, H. axyridis + 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     | *P. japonica, H. axyridis + 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%) > *Menochilus sexmaculatus* (22%) > Ha (17.3%) > C7 (16.7%) | 1-yr sampling on seven fruit orchards; relative abundance | Zhao et al. 2020  |
| Country/Location/Region | Habitat | Most common predator species | Reference |
|-------------------------|---------|-------------------------------|-----------|
| Baoligong National Park, Qinghai-Mountains | 56 coccinellid spp. | H. eucharis (5.3%) > Oenopia kerbi (20.5%) > Ha (0.9%) | Wu et al. 2011 |
| Tibetan plateau, Yunnan Province | > Ha (0.9%) | C7 (69%) > Ha (18%) > Pj (12%) | Osawa 2010 |
| Japan | > Ha (18%) > C7 (17%) > Pj (12%) | Ha (43%) > C7 (12%) > Pj (8%) | Osawa 2010 |
| Kyoto, Botanical garden (1 ha area) | H. axyridis,C7 (69%) > Ha (18%) > Pj (7%). | Ha (54%) > C7 (22%) > Pj (2%) | Osawa 2010 |

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. 1998, Abdel-Salam and Abdel-Baky 2001), pupae of the parasitoid *Trichogramma* sp. (Guo and Wan 2001), or drone bee powder (Niijima 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 *Tuberoccephalus mononis* (Matsumura) (Hemiptera: Aphididae) (Dong et al. 2008).

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 syrius* 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 Katsuhiro 1997). Although *H. axyridis* has a distinct advantage over its competitors in a guild, the incidence of IGP may not be prevalent due to 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*, co-exist 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 syrius* 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* Tiedet (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 Katsuhiro 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* (E) (Araneae: Thomisidae) (Yasuda and Kimura 2001). Numerous parasitoids attack predaecous 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. spinaculus* 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 Lai 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 prepupation 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 (Blekhman 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 (Elmagdy 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 (Bahli 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 endosymbions, parasite loads, and prey defenses (Gegner et al. 2015, Goryacheva et al. 2017, Goryacheva and Blekhman 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.

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