

The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology

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Abstract The harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to Asia but has been intentionally introduced to many countries as a biological control agent of pest insects. In numerous countries, however, it has been

introduced unintentionally. The dramatic spread of *H. axyridis* within many countries has been met with considerable trepidation. It is a generalist top predator, able to thrive in many habitats and across wide climatic conditions. It poses a threat to biodiversity, particularly aphidophagous insects, through competition and predation, and in many countries adverse

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effects have been reported on other species, particularly coccinellids. However, the patterns are not consistent around the world and seem to be affected by many factors including landscape and climate. Research on *H. axyridis* has provided detailed insights into invasion biology from broad patterns and processes to approaches in surveillance and monitoring. An impressive number of studies on this alien species have provided mechanistic evidence alongside models explaining large-scale patterns and processes. The involvement of citizens in monitoring this species in a number of countries around the world is inspiring and has provided data on scales that would be otherwise unachievable. *Harmonia axyridis* has successfully been used as a model invasive alien species and has been the inspiration for global collaborations at various scales. There is considerable scope to expand the research and associated collaborations, particularly to increase the breadth of parallel studies conducted in the native and invaded regions. Indeed a qualitative comparison of biological traits across the native and invaded range suggests that there are differences which ultimately could influence the population dynamics of this invader. Here we provide an overview of the invasion history and ecology of *H. axyridis* globally with consideration of future research perspectives. We reflect broadly on the contributions

of such research to our understanding of invasion biology while also informing policy and people.

Keywords Coccinellidae · Biocontrol · Species traits · Competitive interactions · Invasion history

Introduction

The harlequin ladybird (or multicolored Asian lady beetle), *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to Asia and is a polymorphic, eurytopic species with a broad dietary range (Roy and Brown 2015). It was widely introduced as a biological control agent of pest aphids, but has spread to many countries within which it was not intentionally released (Brown et al. 2008a). The global invasion of *H. axyridis* has been rapid (Brown et al. 2011b). Concerns about the adverse impact of *H. axyridis* particularly on biodiversity but also to people have motivated research across the world. There have been a number of reviews considering the biology and ecology of *H. axyridis* (Kenis et al. 2008; Koch 2003; Koch and Galvan 2008; Majerus et al. 2006; Pell et al. 2008; Pervez and Omkar 2006; Roy and Brown 2015; Sloggett 2012) often from a regional perspective but

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this species has an almost global distribution. Therefore, it is timely to provide a world overview of research and perspectives. Indeed, the collaborative nature of the research from around the world on this species is inspiring. As concerns increased with respect to the threats posed by *H. axyridis*, two working groups were established through the International Organisation for Biological and Integrated Control (within the Global and Western Palaearctic Regional Sections) in recognition of the need for collaborative research on the benefits and risks of exotic biological control agents. One of the first outputs from these working groups was the publication of a special issue on *H. axyridis* including 19 manuscripts representing authors around the world (Roy and Wajnberg 2008). *Harmonia axyridis* as both a biological control agent and an invasive alien species (IAS) has informed a range of applied ecological themes, from risk assessment to processes of invasion; *H. axyridis* is considered by many as a model species for understanding processes of invasion (Roy and Wajnberg 2008).

Here we first consider *H. axyridis* in the context of biological control. We then provide a brief overview of interactions between *H. axyridis* and other species before exploring its current global distribution. We document, on a regional basis, the occurrence and invasion history of *H. axyridis* providing an insight into research priorities and knowledge gaps identified by scientists from around the world. Finally we qualitatively explore the observed traits of *H. axyridis*

from both the native and invaded range reflecting on the potential for future collaborations on a global scale.

Harmonia axyridis and biological control

There has been a long history of using ladybirds as biological control agents against various pest insects around the world, beginning with the successful introduction of the vedalia ladybird, *Rodolia cardinalis* (Mulsant) to citrus groves of California (Caltagirone and Doutt 1989). *Harmonia axyridis* has a wide diet breadth (reviewed by Hodek et al. 2012) including many species of aphids, which are the main prey (Osawa 2000) but also other insect taxa (Ohgushi and Sawada 1998). It has been used extensively in classical, augmentative and conservation biological strategies around the world (Koch 2003; Lombaert et al. 2008). There has been considerable research focus on the pest control services provided by *H. axyridis* in the native range, particularly in China (Wang et al. 2007), but also recently in Japan where adults and larvae of flightless *H. axyridis* derived through artificial selection from a Japanese wild population have been used for biological control of aphids mainly in greenhouses (Seko et al. 2014).

Harmonia axyridis was first introduced as a biological control agent in the USA. It is among a number of introduced species of ladybirds that now dominate in many agroecosystems across the USA

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(Lucas et al. 2007; Obrycki et al. 2009) and *H. axyridis* is considered an important predator of aphid pests in several crops, including pecan (LaRock et al. 2003; Tedders and Schaefer 1994), apple (Brown and Miller 1998), citrus (Michaud 2002) and potatoes (Alyokhin and Sewell 2004). In particular, research has focused on the effect of *H. axyridis* on the suppression of the alien soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) (Ragsdale et al. 2011) in soybean, where *H. axyridis* has recently become one of the most abundant coccinellids (Costamagna and Landis 2007; Gardiner and Landis 2007; Gardiner et al. 2009a; Hesler 2014; Liere et al. 2014; Varenhorst and O'Neal 2012). This system, including the overwintering host of *A. glycines*, the European buckthorn *Rhamnus cathartica* L. (Rhamnaceae) and *H. axyridis*, has been cited as an example of an invasional meltdown, whereby multiple IAS interact synergistically (Heimpel et al. 2010). *Harmonia axyridis* is known to readily consume other predators and parasitoids of aphids (Chacón et al. 2008), but there is a lack of evidence that this impacts pest control in soybean fields (Costamagna et al. 2008).

From the mid 1990s, *H. axyridis* was commercialized by a number of biological control suppliers in Western Europe for augmentative biological control of aphid pests in greenhouse crops and urban ecosystems

(Coutanceau 2006b; Poutsma et al. 2008). Most commercial suppliers in Europe stopped selling the beetle in late 2003 to mid 2004, with the first reports of nuisance problems and increasing concerns about adverse environmental effects of its establishment. In France, the original strain of *H. axyridis* used since 1995 for commercial biological control was replaced in 2000 with a flightless strain developed by INRA (Coutanceau 2006b; Tourniaire et al. 2000). The flightless strain was effectively used to control aphids in hops (Weissenberger et al. 1999). However, the species was never a major player on the European biological control market: at the peak of its commercialisation, it took perhaps 5 % of the market share of aphidophagous natural enemies (De Clercq and Bale 2011).

The role of *H. axyridis* in suppressing pest insects in Europe has received less attention than in the USA. In the Czech Republic it has been reported that *H. axyridis* controls pear psylla, *Cacopsylla pyri* (L.) (Hemiptera: Psyllidae), in commercial orchards more effectively than other ladybird species (Nedvěd 2014). However, much of the research across Europe has considered the occurrence of *H. axyridis* in crop systems without detailed consideration of effects on aphid populations. In Belgium, the population dynamics of *H. axyridis* in crop systems (wheat, corn, broad bean and potato crops)

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was studied through field surveys. It has been shown that *H. axyridis* is recorded in such crops 7–8 days after the dominant native ladybirds (Jansen and Hautier 2008; Vandereycken et al. 2013). A 1-year study involving field observations in wheat and bean crops in southern England reported an absence of *H. axyridis* in wheat (aphid abundance was reported as low), but presence of *H. axyridis* co-occurring with other ladybirds in bean crops (Wells 2011). *Harmonia axyridis* was the most common aphid enemy species in bean crops and the presence of this species was correlated with high aphid abundance (Wells 2011), perhaps unsurprisingly since the prey biomass required by each single larva to reach the adult stage is very high (Soares et al. 2001, 2003, 2004).

Even though *H. axyridis* can be considered an effective biological control agent at least from the USA studies, the Insurance Hypothesis predicts that control will in the long term be better achieved with a diverse array of natural enemies (Loreau et al. 2003). Since *H. axyridis* tends to depress the diversity of coccinellid assemblages (see below), consistently effective biological control may be threatened by the invasion of *H. axyridis*. Further research is needed to unravel the role of *H. axyridis* as a biological control agent of insect pests. Comparison of aphid populations before and after the arrival of *H. axyridis*, or among places with higher and lower abundances of *H. axyridis*, may provide useful information in this respect. Importantly, landscape composition has been found to influence the effectiveness of biological control by *H. axyridis* and other

predators. Indeed, soybean fields embedded within diverse landscapes receive a greater pest control service from aphid predators than fields within simplified agricultural landscapes (Gardiner et al. 2009b) compared to landscapes dominated by forests and grasslands where soybean field size was reduced (Woltz and Landis 2014). Similar studies have been carried out in Chile, in regions where *H. axyridis* dominated the aphidophagous communities and again it has been demonstrated that biological control was related to landscape composition with benefits seen through positive associations with the abundance of woodland and urban habitats, but not with fruit crops, in the landscape (Grez et al. 2014a).

***Harmonia axyridis* and declines of native ladybirds**

The wide diet breadth and recognition that *H. axyridis* is a top predator (Pell et al. 2008) has driven predictions that *H. axyridis* has the potential to adversely affect aphidophagous guilds. A number of large-scale analyses have indicated that declines of native ladybirds correlate with the establishment of *H. axyridis*. Indeed declines of native ladybirds have been reported across the USA (Alyokhin and Sewell 2004; Bahlai et al. 2014; Colunga-Garcia and Gage 1998; Evans 2004; Harmon et al. 2007; Hesler and Kieckhefer 2008; Losey et al. 2014; Majerus et al. 2006; Wheeler Jr and Hoebeke 1995) and Europe (Roy et al. 2012b). Following the establishment of *H. axyridis* in Michigan a decrease in populations of three species of ladybird has been reported: *Brachiacantha ursina* (F.), *Cycloneda munda* (Say) and *Chilocorus stigma* (Say) (Colunga-Garcia and Gage 1998), followed more recently by a decline in *Coleomegilla maculata* (DeGeer) (Coccinellidae) (Bahlai et al. 2015). However, this last study also noted that declines of several species reported previously from the same site (Colunga-Garcia and Gage 1998) appear to have stabilized or reversed, having become statistically undetectable (Bahlai et al. 2015). Also in the USA, Michaud (2002) reported *H. axyridis* to be displacing *Cycloneda sanguinea* (L.) in Florida citrus orchards. In the United Kingdom (UK) there is a strong correlation between the declines of seven out of eight native species of ladybird assessed and co-occurrence with *H. axyridis* (Roy et al. 2012b). In Chilean alfalfa fields the abundance of native ladybird species declined after *H. axyridis* was first observed in this

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crop in 2008. Furthermore, total ladybird species and diversity in alfalfa have also declined during this period (Grez & Zaviezo unpublished data). It is thought that the spread of *H. axyridis* has caused the decline of native species, *Adalia bipunctata* (L.) and *Propylea quatuordecimpunctata* (L.) in the Ukraine (Verizhnikova 2011) and *Coccinella septempunctata* L. and *A. bipunctata* in Moldova (Iazlovețchii and Sumencova 2013), but this requires confirmation through further research.

In contrast, some long-term studies (Honek et al. 2016) have highlighted that some ladybirds native to Central Europe had already been declining before the arrival of *H. axyridis*. Indeed, the diversity of native ladybird communities were similar before (Honek et al. 2014) and after (Honek et al. 2016) the arrival of *H. axyridis* in the Czech Republic. Furthermore, in Switzerland, on-going long-term population studies have highlighted that, so far, only *A. bipunctata* has significantly declined since the arrival of *H. axyridis* (Kenis and Eschen, unpublished data) although risk assessments (Kenis et al. 2010) predicted that three other ladybirds sharing the same ecological niches with *H. axyridis* (*Adalia decempunctata* (L.), *Oenopia conglobata* (L.) and *Calvia decemguttata* (L.)) were at risk.

In Belgium, high niche overlap between *H. axyridis* and generalist native species, particularly *A. bipunctata* and *P. quatuordecimpunctata*, was observed, suggesting a high potential for impact of *H. axyridis* on those species. Large-scale mapping data showed substantial range contraction of *A. bipunctata*, *Adalia decempunctata* (L.), *Calvia quatuordecimguttata* (L.), *Exochomus quadripustulatus* (L.) and *P. quatuordecimpunctata* after the arrival of *H. axyridis*. As a consequence of the invasion, systematic surveying was set up in Brussels using standardized beating of trees in parks, avenues and roadsides. With the exception of *C. quatuordecimguttata*, these abundance data reflected the reported large scale trends (Roy et al. 2012b). *Adalia bipunctata* exhibited a 57 % decline in its extent of occurrence in the last decade and according to a conservative application of the IUCN guidelines has now become a good example of species that was formerly widespread but now meets the criteria of a red list species (Adriaens et al. 2015). However, as for Czech Republic, *A. bipunctata* and *P. quatuordecimpunctata* were already in decline prior to the invasion.

The clear differences in the response of ladybird assemblages to the arrival of *H. axyridis* between

countries highlight the need for comparative studies. In a recent study it was concluded that differences in species trends between central (Czech Republic) and western Europe (UK) could be attributed to suboptimal environmental conditions in the UK, which is the edge of the biogeographic range for many ladybirds, exacerbating the negative effects of *H. axyridis* (Brown and Roy 2015). Such interactions between drivers of change are undoubtedly important in population dynamics, and the negative effects of *H. axyridis* are likely to be the result of a complex range of interactions and processes including resource competition and intra-guild predation (IGP; Majerus et al. 2006).

Long-term and large-scale data on the distribution and abundance of ladybirds are critical for the detection of population changes. To support the collection of long-term survey data, citizen science programmes such as the UK Ladybird survey, Lost Ladybug Project and Buckeye Lady Beetle Blitz in the USA, Chinita arlequin in Chile and the harlequin ladybird survey in Norway have been established to track changes in ladybird populations (Gardiner et al. 2012; Losey et al. 2007; Roy and Brown 2015; Sæthre et al. 2010a, b).

***Harmonia axyridis* and direct competitive interactions**

The majority of research examining interactions between *H. axyridis* and other aphidophagous species has focused on direct interference competition on other ladybirds, proposing that decline is due to strong asymmetric IGP of eggs and larvae in favour of *H. axyridis* (Pell et al. 2008). This hypothesis is supported by many laboratory and field cage studies around the world (Cottrell 2004; Gardiner and Landis 2007; Hoogendoorn and Heimpel 2002; Katsanis et al. 2013; Roy et al. 2008; Snyder et al. 2004; Soares and Serpa 2007; Ware and Majerus 2008; Ware et al. 2009; Yasuda et al. 2004). Under open field conditions in Ohio, USA, eggs of the exotic *H. axyridis* were subject to lower predation relative to the eggs of native species (Smith and Gardiner 2013). However, out of 342 attacks, video surveillance illustrated that only two were attributable to alien ladybirds (*H. axyridis* feeding on conspecific eggs). Instead, a diverse guild of predators (dominated by Opiliones, Tettigoniidae and the native *C. maculata*) were responsible for the

majority of egg attacks (Smith and Gardiner 2013). Importantly, this study accounted only for egg predation but alien and native ladybird species may compete directly through consumption of other life stages. Other tools, such as alkaloid (defensive chemicals within coccinellids) sequestration analyses, frass analysis, and PCR-based gut content analyses, have been developed to quantify the actual extent of interference competition occurring among native and alien species (Brown et al. 2015; Davidson and Evans 2010; Gagnon et al. 2011; Hautier et al. 2008, 2011; Sloggett et al. 2009; Thomas et al. 2013). For example, Hautier et al. (2011) found that 20.5 % of 590 *H. axyridis* larvae in Belgium tested positive for native ladybird alkaloids. Thomas et al. (2013) detected the DNA of native ladybirds within *H. axyridis* in the UK, with 3.7–22.7 % of 156 *H. axyridis* found to have consumed native species over 3 years. Gagnon et al. (2011) used molecular gut content analysis to illustrate that IGP among larval ladybirds in soybean fields can be very high; 52.9 % of sampled ladybirds contained the DNA of one or more other ladybird species. PCR primers have been developed and used to track aphid and ladybird predation by *H. axyridis* fourth-instar larvae collected in lime trees in Italy, and it was found that 7 % of sampled individuals contained the DNA of one of two native ladybird species (Rondoni et al. 2015).

There has been less research on the interactions between *H. axyridis* and species within the aphidophagous guild beyond ladybirds (Pell et al. 2008). However, laboratory and field studies have also indicated direct interactions with non-coccinellid aphidophagous predators. *Harmonia axyridis* is an intra-guild predator of *Episyrphus balteatus* (DeGeer); (Diptera: Syrphidae) with the strength of this asymmetric interaction increasing with developmental stage of *H. axyridis* and decreasing in the presence of extraguild prey (Ingels and De Clercq 2011). The aphid-specific pathogenic fungus *Pandora neoaphidis* (Remaudiere and Hennebert) Humber (Zygomycota: Entomophthorales: Entomophthoraceae) is consumed by *H. axyridis* (Roy et al. 2008) whereas most other aphid predators avoid consumption of infected aphids (Roy et al. 1998). Interestingly cage experiments in Italy have been used to study predation on immature stages of *H. axyridis*, and it has been observed that ants exhibit high levels of predation (Burgio et al. 2008a). Further research has demonstrated the influence of many factors on IGP, including intrinsic (such as

feeding history of the species) and extrinsic (such as habitat complexity), and highlighted the importance of addressing such factors when considering the ecological relevance and extent of IGP (Ingels et al. 2015).

***Harmonia axyridis* and indirect competitive interactions**

Harmonia axyridis may also adversely affect aphidophagous species through exploitative competition for shared resources (Evans et al. 2011). Studies to date have failed to show that *H. axyridis* negatively affects native North American ladybirds through exploitative competition among larvae (Hoogendoorn and Heimpel 2004; Yasuda et al. 2004), however, field and microcosm studies reveal reduced fitness in the predatory bug *Anthocoris nemoralis* (F.) (Hemiptera: Anthocoridae) due to competition with *H. axyridis* (Howe et al. 2015, 2016). Evans (2004) proposed that following the introduction of alien competitors (specifically *C. septempunctata*), native species abandoned croplands due to increased competition for shared prey. Adults of native species were thought to be displaced to ancestral (refuge) habitats not heavily exploited by alien competitors (Evans 2004; Snyder 2009). Evans (2004) tested this hypothesis by increasing aphid abundance in a Utah alfalfa fields and found that native ladybirds were drawn back into the field, apparently from refuges maintained in the surrounding landscape. In Japan *H. axyridis* coexists with other predators within natural habitats, without adverse negative impacts on co-occurring species (Osawa 2011).

Alien ladybirds and landscape-scale processes

Landscape change can strongly influence species declines within a region (Lindborg and Eriksson 2004). Factors such as habitat degradation, reduction of habitat patch size, and increased isolation of habitats (loss of connectivity) can also lead to declines in the abundance and diversity of coccinellid species within a landscape (Gardiner et al. 2009a; Grez et al. 2013, 2014b). Ladybirds may forage across several habitats within a given landscape including forests, grasslands, and croplands. Landscape changes that alter the distribution of these habitats may affect ladybirds by influencing prey populations, overwintering habitats, or by facilitating the invasion of alien competitors.

Observations from several countries suggest that a high proportion of native ladybirds occur in less disturbed habitats, while a high proportion of alien ladybirds (including *H. axyridis*) occurs in human-modified habitats (Grez et al. 2013; Panigaj et al. 2014).

Landscape composition and heterogeneity can also affect competitive interactions among coccinellids (Gardiner et al. 2009a). In the USA, alien species were more abundant within soybean fields embedded within forested landscapes, and native species more common in agricultural landscapes with significant forage and grassland habitat. A large-scale study assessing the influence of landscape factors on the spread of *H. axyridis* across the UK indicated that coniferous woodland may negatively affect the spread of this species (Purse et al. 2014). Further research is needed to examine how the composition of the surrounding landscape influences the stability of native populations in the invaded regions.

***Harmonia axyridis* as a household and agricultural pest**

Many ladybirds in temperate regions migrate for overwintering to elevated and conspicuous elements in landscape, or even to hill tops (Hodek et al. 2012). There they seek crevices in rocks, in bark of prominent trees and other shelters including south-facing anthropogenic structures such as buildings and monuments (Koch and Galvan 2008; Roy and Brown 2015; Wang et al. 2011). *Harmonia axyridis* forms large aggregations during the winter months across the native and invaded range in natural areas but also within homes and other structures (Nalepa 2007; Roy and Brown 2015). A recent study from Poland highlighted the use of wind turbines as overwintering sites for *H. axyridis* (Dudek et al. 2015). It shows hypsotactic behaviour (moving towards prominent objects on the horizon) and a clear preference for contrasting visual elements; vertically positioned stripes being more attractive than horizontal ones (Nalepa et al. 2005; Obata 1986). The relative attractiveness of different surface colours has been studied; white is the most attractive colour followed by yellow and black then green then red and finally natural wood (Wang et al. 2011). Volatile aggregation pheromones are not involved in this orientation (Nalepa et al. 2000) but it is apparent that contact chemoreception is important in the establishment of large aggregations (Durieux et al. 2012).

Harmonia axyridis accounts for 97 % of observations from houses contributed by citizen scientists to the US Lost Ladybug Project (Ramsey and Losey 2012). Infestations in homes can cause staining damage to carpet and furnishings and cause allergic reactions (Goetz 2008; Koch and Galvan 2008), but most often are considered a nuisance. Additionally, although this species does not have a greater propensity to bite humans than other ladybirds, its propensity to aggregate in dwellings in high numbers has resulted in a significant increase in the number of ladybird bites reported (Ramsey and Losey 2012). After infestation of the intensive care unit in a large hospital in Austria, counteractive measures including relocation of patients and temporarily closure of the station generated considerable financial costs. Management tactics have been developed to mitigate such nuisance problems (Kemp and Cottrell 2015).

Harmonia axyridis has been reported to feed on many fruit crops in many parts of the world including grapes, stone fruit, apples, pumpkins and berry crops (Koch et al. 2004a). Depending on fruit type, this feeding damage includes primary injury as well as secondary feeding on wounded tissue. In China *H. axyridis* has been documented foraging on pollen, nectar and young plant tissues, occasionally causing serious damage to fruits (Guo and Wan 2001; Yang et al. 2006). In contrast in Japan *H. axyridis* does not consume orchard fruits and overwintering *H. axyridis* are not regarded as a household pest. However, economically, *H. axyridis* presents the largest threat as a contamination pest in wine grape production (Koch and Galvan 2008). Beetles can be found within vineyards largely between the onset of ripening and harvest (Galvan et al. 2008). Adults aggregate and feed on injured fruit clusters (Koch and Galvan 2008). When fruit are harvested and crushed, *H. axyridis* release methoxypyrazines (MPs) which create an unpleasant odour and taste in the wine produced (Botezatu et al. 2013; Galvan et al. 2008). In the Midwestern USA, the dramatic increase in *H. axyridis* in wine grapes generally follows population declines in nearby soybean and maize fields (Bahlai and Sears 2009; Galvan et al. 2006, 2008); however, more research is necessary to document this dispersal hypothesis.

A push–pull strategy including artificial injury of selected fruit clusters on the vineyard margin and spraying the adjacent rows with bisulphite has been

proposed as a management option (Glemser et al. 2012; Nedvěd 2014). In addition, progress has been made in developing both natural and synthetic corks that can significantly reduce MP concentrations in wine (Pickering et al. 2010). However, more research is needed to evaluate this approach for additional varietal sources and cost effectiveness. The establishment of *H. axyridis* in regions where the production of wine is economically important, including Crimea, the Caucasus, Canada, Europe, South Africa and South America, continues to be a concern, and close monitoring of the populations in these countries is critical.

Global distribution and regional research priorities

Harmonia axyridis has become one of the world's most widely distributed ladybirds (Fig. 1) and is now found on all continents except Antarctica and notably is absent from a few large countries such as Australia. Outside of its native range (Asia), it has become very widely established in North America, South America and Europe (Fig. 2), and in limited parts of Africa. There is a small distance between the western edge of the native range and the eastern edge of the invaded range (see Russia and adjacent countries below), and it seems inevitable that these populations will meet in the near future.

In this section we document the distribution of *H. axyridis* around the world and its invasion history (summarized in Table 1), including the perspectives on regions where it has failed to invade. Additionally, current and future research priorities in different countries are presented.

Asia

Harmonia axyridis is native to East Asia (Mongolia, parts of China and Russia, northern Vietnam, Japan and Korea; Fig. 1).

China

Harmonia axyridis has a wide geographical range in China, especially in the north (Wang et al. 2007).

Current research on *H. axyridis* in China is mainly focused on agricultural applications, including the development of artificial diet for *H. axyridis* to maximise production of this species for field release in augmentative biological control (Wang et al. 2007). *Harmonia axyridis* has also been used extensively for testing pesticides and specifically examining the sensitivity of natural enemies to pesticides (Tang et al. 2014). There is also ongoing research on the genetics of *H. axyridis* colour polymorphism, specifically how colour variation interacts with environmental factors.

Japan

In Japan, *H. axyridis* occurs on the islands of Hokkaido, Honshu, Shikoku, Kyushu, Tsushima, Iki and Gotoh, while its sibling species *H. yedoensis* (Takizawa) occurs on Honshu, Shikoku, Kyushu, Yakushima and the Ryukyus (Kurosawa et al. 1985). Future research in Japan will focus on intensive field studies to establish the mechanisms which enable coexistence of *H. axyridis* and other ladybird species in its native range.

Asian part of Russia, Kazakhstan and Kyrgyzstan

The northern part of the native range of *H. axyridis* occupies the south of Siberia and the Far East. The type locality of the species is in Siberia (Pallas 1771). The geographical distribution and colour variability of this species was first studied in the 1920s (Dobzhansky 1924). A recent map of the native range has been compiled (Orlova-Bienkowskaja et al. 2015). *Harmonia axyridis* populations west of Baikal Lake (in West Siberia and the western part of East Siberia) differ both genetically and morphologically from those living east of Baikal (Lombaert et al. 2011, 2014; Vorontsov and Blekhan 2001).

The native range of *H. axyridis* includes in the Altai Mountains, situated in north-eastern Kazakhstan and West Siberia. In some recent studies, the south-east of Kazakhstan was regarded as part of the native range (Loiseau et al. 2009; Lombaert et al. 2011, 2014). However, this is incorrect because *H. axyridis* was not recorded in the south-east of Kazakhstan in the nineteenth century or in the first half of the twentieth century. In 1968–1970 attempts to introduce *H. axyridis* from the Far East to the south-east of



Fig. 1 Global distribution of *H. axyridis*

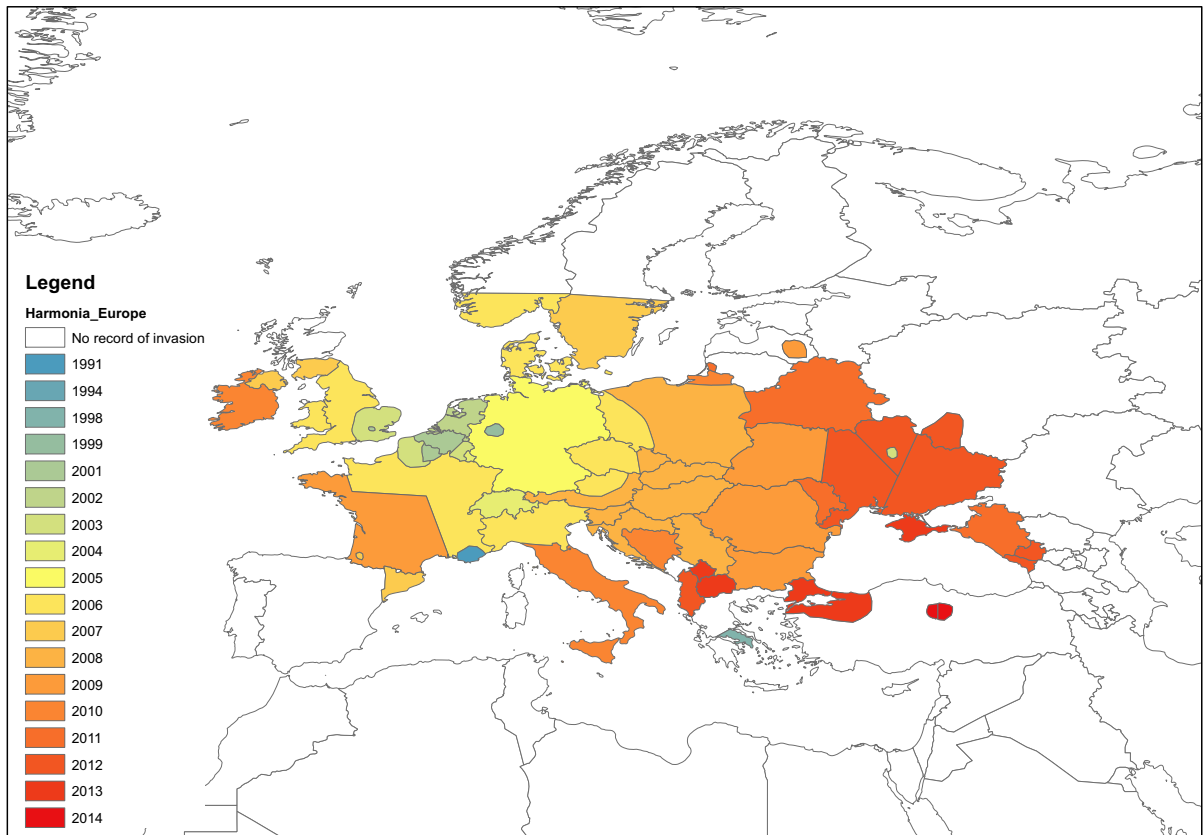


Fig. 2 European distribution of *H. axyridis*

Kazakhstan for biological control of aphids (Savojnskaja 1971) failed. Now *H. axyridis* is a common species in the south-east of Kazakhstan and was recently detected in the neighbouring region of Kyrgyzstan. Both morphological and genetic studies strongly indicate that the *H. axyridis* occurring in this region are not descendants of the released beetles, since current populations are similar to West-Siberian populations and differ from Far East populations. It is hypothesised that *H. axyridis* appeared in south-eastern Kazakhstan and Kyrgyzstan after the construction of the Turkestan-Siberian Railway, and that the beetles spread along this railway (Orlova-Bienkowskaja et al. 2015).

European part of Russia, Moldova, Ukraine and Belarus

Releases of *H. axyridis* for biological control of aphids in the Soviet Union began about 80 years ago.

Attempts to introduce *H. axyridis* were made in Transcaucasia in the 1930s, in the Chernovtsy region (Ukraine) in 1964, in the Kiev region (Ukraine) in the 1960s, in Crimea in 1969, in the Tashkent region (Uzbekistan) in 1969, in Minsk (Belarus) in 1968–1970, in south-eastern Kazakhstan in 1968–1970 and in Adjara and Mtsheta region (Georgia) in 1982–1988. It is thought that none of the intentionally released populations established (Izhevsky 1990; Verizhnikova and Shylova 2013). Established populations are thought to have originated from secondary spread eastward of *H. axyridis* from western Europe to European Russia and neighbouring countries. Established populations were detected in the Kaliningrad region (Russian enclave in the Baltic region; Zakharov et al. 2011). Recently, *H. axyridis* has been observed spreading rapidly in the Caucasus and the south of European Russia (Orlova-Bienkowskaja 2014). Established populations have been found in Adygea, Krasnodar region, Abkhazia, the Stavropol region, Georgia (Belyakova and Reznik 2013), Crimea

Table 1 Invasion characteristics and ecological attributes of *Harmonia axyridis* documented from countries around the world

	Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies
China	Native	Native	Native	Wide Agricultural Grasslands Woodlands	Wide Aphids Mites Coccids Pollen Young plant tissues	Braconidae <i>Medina luctuosa</i> <i>Phalacrotophora philaxyridis</i> <i>Hesperomyces virescens</i> <i>Strongygaster triangulifera</i> Birds
Japan	Native	Native	Native	Wide Urban habitats Parks Backyards Agricultural Gardens (mainly on trees and shrubs)	Wide Aphids Ladybird larvae	<i>Dinocampus coccinellae</i> <i>Phalacrotophora</i> sp.
Siberia and the Far East	Native	Native	Native	Wide Deciduous Coniferous forests Gardens Urban habitats Grasslands Fields	Wide Aphids Coccids Psyllids Coccinellids	Birds <i>Dinocampus coccinellae</i>
European Russia	Multiple intentional releases in the Caucasus starting in 1930s (not established). First population seen in wild in 2010 in the west. Invasive population likely secondary spread from Poland	Established in the west and in the south. Individual specimens found in centre of European Russia	Range expansion in the south estimated at 300 km per year. Expansion to the central regions is not yet known	Wide Urban habitats Forests Fields Gardens Floodplains	Wide Aphids Coccids Psyllids Coccinellids	Unknown

Table 1 continued

	Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies
USA and Canada	Multiple intentional releases across North America, starting California in 1916. Introduced into North America throughout 1980s. First population seen in wild in 1988	Found across USA by mid-1990s. First seen in Canada in 1994	Initial range expansion in southeastern USA estimated at 309 km per year	Wide Agricultural Woodlands Grasslands Residential and urban landscapes	Wide Many Hemiptera (i.e. aphids, psyllids and coccids) Tetranychidae Immature stages of Lepidoptera and Coleoptera (i.e. Coccinellidae, Chrysomelidae, Curculionidae) Fruit crops Pollen Nectar	<i>Coccipolipus hippodamiae</i> <i>Hesperomyces virescens</i> <i>Strongygaster triangulifera</i> <i>Dinocampus coccinellae</i>
Chile	Eastern North USA Intentional introduction of flightless strain from France in 1998 but this did not establish	Wild population of flying strain discovered in 2003	Expanded from a range of 250 km (north to south) near Santiago, to 2600 km (north to south); approximately at a rate of 160 km per year, mostly towards south	Agricultural (particularly abundant in alfalfa during spring and autumn but also present in wheat) Houses (autumn and winter) Vineyards Orchards Gardens Native matorral	Wide Mostly seen feeding on aphids <i>Aphis craccivora</i> <i>Acyrtosiphon pisum</i> <i>Chromaphis juglandicola</i> <i>Chaitophorus leucomelas</i>	<i>Dinocampus coccinellae</i>

Table 1 continued

	Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies
Belgium	Intentional introduction as biocontrol agent in 1997	First wild population found in 2001	Range expansion of 189 % on average per year (2002–2006)	Agricultural (dominant in corn) Urban and anthropogenic habitats Less abundant in (semi-) natural areas Predominantly on trees and shrubs but also on herbs	Wide	<i>Dinocampus coccinellae</i> <i>Hesperomyces virescens</i> Araneidae
Czech Republic	Intentional introduction as a biocontrol agent in early 2000s, however this population did not establish Invasive population likely secondary spread from Germany	First establishment seen in 2006	First invasive population seen in 2006, by 2009 it could be found in most disturbed habitats across the country	Urban Abundant on deciduous trees and shrubs but also ruderal herbs	Wide Mostly aphids Many psyllids e.g. <i>Cacopsylla pyri</i>	<i>Hesperomyces virescens</i> <i>Passer montanus</i> Other parasites and parasitoids only occasionally
Denmark	Unintentional introduction Presumed to have arrived from Germany	First recorded in 2006	Expanded from Copenhagen east and west, however establishment is limited in the north of the country	Urban Agricultural Parks and gardens	Wide Aphids (<i>Eucallipterus tiliae</i>) Hemiptera (<i>Anthocoris nemoralis</i>)	<i>Beauveria bassiana</i> <i>Isaria farinosa</i> <i>Lecanicillium</i> spp.
France	Intentional introduction in 1982 <i>H. axyridis</i> sampled across France all belong to a single genetic unit that has invaded the western part of Europe. It bears traces of genetic admixture between an eastern North American wild source, and a biocontrol strain used in Europe	Populations started to spread in 2004	Dispersal was greatly aided by anthropogenic factors, especially the relative surface area of urban habitats, and average summer temperatures not being too high or low	Urban Parks and gardens Agricultural	Wide Most aphids Many psyllids	Not recorded

Table 1 continued

Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies
Germany	Intentional introduction during end of 1990s Unclear, if invasive populations derives from intentional introductions or spread	First reports from Frankfurt City in 2000 followed by rapid spread across Germany	Agricultural Gardens Vineyards Orchards	Wide Many aphid species, e.g. on cereals (wheat, corn), <i>Aphis fabae</i> , other plant sucking insects <i>Eriosoma lanigerum</i> on apple Grape phylloxera (<i>Daktulosphaira viticollae</i>) Pollen Fruit sap (e.g. from grape berries)	<i>Hesperomyces virescens</i> <i>Dinocampus coccinellae</i> Allantonomatidae
Italy	Intentional introductions from 1995 to 1999 Presumed that wild populations originated from biocontrol releases or secondary spread from France, Switzerland and other parts of Italy	Population first recorded as in wild in 2006 Expanded from first wild recorded individuals in 2006 to cover 18 of 20 Italian regions in 2015	Agricultural Gardens Vineyards Orchards	Wide Aphids Psyllids Coccids <i>Metcalfa pruinosa</i> Pollen	<i>Dinocampus coccinellae</i> <i>Phalacrotophora fasciata</i>

Table 1 continued

Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies
The Netherlands	Intentional introduction Presumed secondary spread from Belgium	Expanded from the first record in 2002 to spread rapidly from 2004 onwards, from south to north. By 2006 establishment across the entire country	Agricultural (dominant in corn) Urban Predominantly on trees and shrubs but also on herbs in urban and anthropogenic habitats, less abundant in (semi-) natural areas	Wide Including cannibalism (observation of specimens eating while other specimen was laying eggs)	<i>Araneus diadematus</i> (autumn), <i>Coccipolipus hippodamiae</i> (winter) <i>Dinocampus coccinellae</i> (summer, winter) <i>Hesperomyces virescens</i> (summer, winter) <i>Parasitylenchus bifurcatus</i> (winter) <i>Phalacrotophora fasciata</i> <i>Phalacrotophora</i> sp. (spring, summer) <i>Dinocampus coccinellae</i>
Norway	Unintentional introduction Oslo in 2006, arrived as a stowaway on horticultural plants, <i>Thuja</i> sp. (Cupressaceae) imported from the Netherlands	Limited to urban and suburban regions, and not recorded from commercial crops or in natural habitats	Urban Gardens Parks Most records from the wider Oslo area. No reports from agricultural or horticultural crops	Not measured	
Slovakia	Unintentional introduction Presumed secondary spread from Austria, Poland and the Czech Republic	Expanded from the first record in 2008 across the entire country by 2009 at a rate of about 200 km per year. Local topography played a role in the spread	Urban Orchards Deciduous and lowland pine forests Vineyards Agricultural	Wide Hemiptera Larvae of Lepidoptera Dying flightless adults of Diptera	<i>Chrysoperla carnea</i> <i>Passer montanus</i>

Table 1 continued

Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies	
Switzerland	Unintentional introduction Presumed secondary spread from Germany and France	First recorded in 2004, with very large populations found in 2006	Expanded from the first record in 2004 to rapidly invade all areas of low and middle altitudes of the country by 2006	Urban Woodland (particularly on broadleaved trees in woodlands and urban areas, but much less frequent on conifers, meadows or in agricultural habitats)	Not measured	Not recorded
UK	Unintentional introduction Presumed secondary spread from mainland Europe particularly Belgium and France	First recorded in 2003 and as established in 2005	Expanded from first record in 2003 at more than 100 km per year in the UK, both via flight and anthropogenic transport	Urban Parks and gardens Woodlands (mainly deciduous) Grasslands Agricultural	Wide Hemiptera Lepidoptera Coleoptera	<i>Dinocampus coccinellae</i> <i>Hesperomyces virescens</i> <i>Homalotylus flaminius</i> <i>Medina separata</i> <i>Oomyzus scaposus</i> <i>Phalacrotophora berolinensis</i> <i>Phalacrotophora fasciata</i> (lower susceptibility of <i>H. axyridis</i> compared to other species evident from laboratory and field studies)

Table 1 continued

Origin	Establishment	Spread	Habitat breadth	Diet breadth	Natural enemies
South Africa	Intentional introduction c. 1980; no establishment	Spread rapidly, established largely in cooler and more mesic regions. Initial spread of up to 500 km per year likely human-assisted	Gardens (urban and rural)	Wide	<i>Dinocampus coccinellae</i>
	Present invasion likely from unintentional introduction (unknown whether multiple)		Orchards (deciduous and subtropical fruit)	Field observations include: Aphids	<i>Hesperomyces virescens</i>
	Eastern North America (genetic analysis of 4 South African populations)		Vineyards	Coccinellids	
			Field crops		
			Pine plantations		
			Indoors		
			Untransformed fynbos, grassland, moist savanna		
			Frequently on oak trees, ornamental conifers, garden roses		

It is important to note that various approaches have been adopted for categorising the attributes and so direct comparison between countries is not always possible. Standard approaches to capturing this information would be useful to enable quantitative assessments on a global scale. Natural enemies have not been systematically surveyed in most countries and so the lists represent opportunistic observations. The origin is often inferred from geographic proximity to other countries but in some cases through molecular analysis. Spread has been measured as distance (km per year) for some countries. Broad habitat categories are provided but harmonization of terminology is recommended. Diet breadth has not been systematically analysed for each country and the lists represent opportunistic observations. Taxonomy for species is provided at first mention within the main text other than Aphididae: *Aphis craccivora* Koch, *Aphis fabae* Scopoli, *Chaitophorus leucomelas* Koch, *Chromaphis juglandicola* (Kaltenbach), *Eriosoma lanigerum* (Hausmann); *Eucallipterus tiliae* (L.); *Daktulosphaira vitifoliae* (Fitch) (Phylloxeridae); *Araneus diadematus* Clerck (Araneidae) (*Chrysoperla carnea* (Stephens) (Chrysopidae); *Homalotylus flaminus* (Dalman) (Encyrtidae); *Medina luctuosa* (Meigen); *M. separata* (Meigen); *Strongygaster triangulifera* (Loew) (Tachinidae); *Phalacrotophora philaxyridis* Disney (Phoridae); *Metcalfa pruinosa* (Say) (Flatidae); *Oomyzus scaposus* (Thomson) (Eulophidae); *Passer montanus* (L.) (Passeridae)

(Rybalchenko, personal communication), Daghestan (Ilyina, personal communication) and Rostov region (Arzanov, personal communication). Individual specimens of *H. axyridis* have also been found in the central belt of European Russia (Belgorod and Lipetsk regions; Orlova-Bienkowskaja 2013; Ukrainsky and Orlova-Bienkowskaja 2014), but it is unknown if the species is established there.

In 2003, several specimens of *H. axyridis* f. *spectabilis* were found in the wild in Kiev (Ukraine) and since 2007 a stable population of *H. axyridis* has existed there (Verizhnikova and Shylova 2013). In 2009 *H. axyridis* was detected in several locations in western Ukraine, and there has been rapid expansion since, with the species now abundant all over the country (Nekrasova and Tytar 2014). The spread of *H. axyridis* has been so rapid that it has been observed to occur across a whole country before being detected: *H. axyridis* was not detected in Moldova until 2011, when it had already become common throughout the country (Timuş and Stahi 2013).

Harmonia axyridis has been recently detected in Belarus, in the Brest region. The first specimen was found in 2011, but 14 individuals were subsequently found in 2014 (Lukashuk and Ryndevich, unpublished).

Current research in Russia and the Ukraine relates to the development and effects of photoperiod on development and maturation (Belyakova and Reznik 2013; Reznik et al. 2015), genetics (Zakharov et al. 2011), morphological variability (Blekhnman 2008), population dynamics (Nekrasova and Tytar 2014) and current expansion of the range in Russia and adjacent countries (Ukrainsky and Orlova-Bienkowskaja 2014). There is also considerable interest in elucidating the routes of invasion by genetic methods as has been done for many other regions (Lombaert et al. 2014). It is possible that the populations in the Caucasus and in the south of European Russia include hybrids between invasive European individuals and those introduced from the Far East for use in biological control. As the secondary range is expanding eastwards, it is predicted that it will soon reach the western border of the native range. Thus there is an opportunity to observe the consequences of interactions between native and invasive populations in West Siberia.

North America

Harmonia axyridis was repeatedly introduced throughout the twentieth century to the USA with the aim of establishing populations (Gordon 1985; Harmon et al. 2007; Koch et al. 2006b). Intentional releases of *H. axyridis* include a number of states but notably California in 1916, and multiple eastern states from 1978 to 1992 (Chapin and Brou 1991; Gordon 1985; McClure 1987; Tedders and Schaefer 1994). *Harmonia axyridis* was first detected beyond intentional release sites in the United States in 1988 in south-eastern Louisiana and eastern Mississippi (Chapin and Brou 1991). A second, independent set of releases led to establishment in the 1980s in the Pacific Northwest (LaMana and Miller 1996; Lombaert et al. 2010, 2014). It is unknown whether all established populations resulted from these releases or from additional, accidental introductions. Nonetheless by the mid-1990s, *H. axyridis* had been found across the country with detection reports from 45 of the 48 contiguous states by 2007 (Dreistadt et al. 1995; Hesler et al. 2001; Krafstur et al. 1997; LaMana and Miller 1996; Mizell III 2007) and most recently from Montana in 2009 (Foley et al. 2009) and Arizona in 2008 (Fothergill et al. 2010). *Harmonia axyridis* was first detected in Canada in 1994 (Coderre et al. 1995). Currently this species is found throughout most of North America north of Mexico with Labrador, Saskatchewan, Alaska and Wyoming the only areas where it has not yet been reported (Foley et al. 2009; Fothergill et al. 2010; Hicks et al. 2010; Koch et al. 2006b). *Harmonia axyridis* is also established and widespread in Mexico (Brown et al. 2011b).

Outside of the native range, North America has the longest history of experience with *H. axyridis* and may serve as a case study of potential impacts, positive or negative, that this species may cause in other invaded areas (Koch et al. 2006a; Koch 2003; Koch and Galvan 2008). Some recent lines of research in North America are reviewed elsewhere in this paper. Briefly, research continues on attaining benefits from *H. axyridis* as a biological control agent of pests, and on understanding and minimizing adverse impacts of the invasion (pest of fruit and wine production, nuisance household invader, and impacts on native fauna).

South America

Harmonia axyridis is reported in most countries in South America (Amat-García et al. 2011; González and Kondo 2012; Koch et al. 2011; Kondo and González 2013; Nedvěd and Krejčík 2010; Saini 2004; Solano and Arcaya 2014). Based on factors such as climate and habitat, it has been predicted that *H. axyridis* would become established across broad areas of South America (Koch et al. 2006b). The invasion by *H. axyridis* has been followed intensively in Chile.

Chile

In 1998, a flightless strain of *H. axyridis* was introduced from France to central Chile for biological control in greenhouses, but those populations did not establish (Grež et al. 2010; Table 1). In 2003, large numbers of flying *H. axyridis* associated with aphids in poplar trees were reported near the release sites. In 2008, surveys of ladybird populations in alfalfa revealed only one individual *H. axyridis* (from a sample of approximately 90,000 ladybirds), but rapid population increase was observed over the next 2 years in alfalfa and other habitat or crop types (Grež et al. 2010). *Harmonia axyridis* is currently one of the two most abundant species in alfalfa fields in central Chile, representing 50–90 % of ladybirds (Grež et al. 2014a, b). It is expanding into other habitats, including native vegetation, such as sclerophyllous matorral, although at very low densities (Grež et al. 2013). *Harmonia axyridis* is spreading toward southern Chile, colonizing regions with colder climates. In contrast, few records are reported towards northern Chile, where the Atacama Desert is probably acting as a barrier for its invasion. From its original distribution in 2010, covering a range of 250 km (north to south) near Santiago, it has expanded its distribution to 2600 km (north to south), and from sea level to >3000 m a.s.l., with a north to south spread of approximately 160 km year⁻¹. Genetic analyses suggest that current Chilean populations come from the East North America strain (Lombaert et al. 2014), representing an accidental introduction. Only f. *succinea* has been found in Chile.

Current research in Chile relates to the impacts of this species on the diversity of ladybird assemblages and abundance, including native species, in different

habitats, as well as its potential damage to vineyards. There are also extensive field and laboratory experiments in progress to assess IGP and competition as mechanisms for understanding the dominance of *H. axyridis* over other ladybirds. Studies of physiological performance and life history traits under different temperature conditions in the laboratory have also been carried out (Barahona-Segovia et al. 2015). The invasion process is being systematically tracked through surveys coordinated by Grež and Zaviezo, including data from the Surveillance Department of the National Agrarian and Livestock Service (SAG), and from media and social networks specifically developed for this purpose (web page: <http://www.chinita-arlequin.uchile.cl/>; Facebook: <https://www.facebook.com/chinita.arlequin>; twitter: <https://twitter.com/chinitaarlequin>). The high interest and participation of citizens through these media suggest that the presence of *H. axyridis* is of growing concern to Chileans.

Spatial distribution models are also being developed to forecast the future distribution of *H. axyridis* in the country. Chile is a long (4329 km) and narrow (180 km on average) country, isolated by the Atacama Desert to the north, the Pacific Ocean to the west, and the Andes mountain range to the east. The Chilean environment has strong latitudinal gradients in abiotic conditions, from the most arid desert in the world in the North, followed by a semi-arid region, Mediterranean type ecosystems in central Chile, the temperate rainforests toward the South, and the southernmost sub-Antarctic ecosystems (Luebert and Pliscoff 2006). This gradient offers a unique opportunity to study how climate modulates the distribution and abundance of this invasive alien species. Also, along this gradient, a highly diverse native fauna of coccinellids (~115 species; González 2008) offers a unique opportunity to evaluate the possible changes of native communities after *H. axyridis* arrival.

The main gaps in knowledge in Chile relate to natural enemies and possible control or containing methods. The only observed natural enemy thus far is the parasitoid *D. coccinellae*. Also, there are many unanswered questions in relation to the ecology and biology of *H. axyridis* during summer time, when this species disappears from crops, apparently estivating or migrating to other, as yet undetermined, locations. Its role as a biological control agent of aphids and other pests is still unknown.

Europe

A network of scientists was established through a working group (Benefits and Risks of Exotic Biological Control Agents) of the Western-Paleartic Regional Section of the International Organisation of Biological Control in response to the rapid spread of *H. axyridis* throughout Europe. Consequently there has been ongoing collaborations to map the distribution throughout Europe (Brown et al. 2008a) and so here we present information reflecting this activity on a country by country basis. There is considerable scope to enlarge the network and research collaborations and we look forward to doing so in the coming years.

Austria

Harmonia axyridis was first recorded in eastern Austria in 2006 (Rabitsch and Schuh 2006) and soon reported from other provinces, where it may have been present but undetected for some time. It was never imported or sold as a biological control agent in the country and the arrival via natural spread from north-western Europe is most likely. After almost a decade, however, the species has been found in all federal provinces and there is no doubt that it has become the most abundant ladybird species in Austria.

Unfortunately, no systematic surveillance or monitoring data are available to trace the expansion within Austria or to document any impact on native biodiversity. Personal observations from entomologists, however, indicate that the species has strongly increased in abundance and range over the last decade. The establishment and use of citizen science initiatives in gathering information are currently under development.

Belgium

In Belgium, *H. axyridis* was first applied as a biological control agent in 1997. The species was first observed in the wild in 2001 (Adriaens et al. 2003) and this led to the end of its commercial use in Belgium. In less than 5 years the species invaded the entire country, its distribution covering all Belgian ecoregions (Adriaens et al. 2008). The area of occupancy showed an average rate of increase of 189 % (5000 km²) per year from 10,000 km² in 2002 to

31,000 km² in 2006. *Harmonia axyridis* has become the most abundant species in (semi-)natural systems and also dominates the aphidophagous guilds in certain agro-ecosystems (Vandereycken et al. 2013).

At the time of arrival and spread of *H. axyridis* in Belgium a country-wide validated citizen-science survey (Gardiner et al. 2012) focussing on the ecology and distribution of 40 native ladybird species was running. This allowed almost real-time monitoring of this insect invasion as well as detailed analysis of niche overlap with native species (Adriaens et al. 2008). Future research on the decline of native coccinellids should also consider factors such as land use change, climate change, habitat quality and effects of pesticides as potential contributors to this phenomenon.

Czech Republic

Although *H. axyridis* was released in the Czech Republic for protection of hops in the early 2000s, it did not establish. The first occurrence of the invasive population dates back to 2006. In 2007, it occurred near the western borders of the country and in a few cities, but in 2008 it was found in many cities and towns including the eastern-most (Špryňar 2008). In 2009, the species could be found in most anthropogenic-altered landscapes, but not in remote areas such as mountains over 1100 m, continuous forests and closed military zones. Mass infestation of houses during autumn migrations raised public awareness and a few cases of biting and allergic reactions were reported. Unintended transfers of single specimens over hundreds of kilometres were recorded (Nedvěd 2014).

Denmark

Harmonia axyridis was first recorded in Copenhagen 2006, and presumed to have arrived from Germany (Brown et al. 2008a; Pedersen et al. 2008). In the following years the beetle spread within the Greater Copenhagen area, becoming established across the island of Zealand. By 2007/8, its spread continued westwards to the islands of Lolland, Langeland, Ærø, and in the east to Bornholm (perhaps arriving from Poland or Germany) where populations are now established (Howe 2015; Howe et al. 2015; Steenberg and Harding 2009b; Steenberg et al. 2009). By 2008, *H. axyridis* had reached Jutland in the far west of

Denmark (Steenberg et al. 2009). The most northern record to date (latitude 57°N) was from produce in a supermarket, highlighting the potential for spread through anthropogenic pathways. Data from Zealand indicates stable populations with *H. axyridis* dominating ladybird assemblages where established. Greatest densities occur within urban areas of central Copenhagen (Ravn and Howe, unpublished data).

It is interesting to note that the distribution of *H. axyridis* in Denmark is limited in the north of the country. Indeed, following 10 years' of establishment within Denmark, aside from the aforementioned supermarket record there are no records of *H. axyridis* north of 56°N (Ravn and Howe, unpublished data), which corresponds with a lack of records from Scotland (UK). Whether this represents a true limit to the northern distribution attributable to present climatic conditions requires further research, particularly in relation to future predictions of spread based on expected climate warming.

France

In France, *H. axyridis* was first introduced for biological control in 1982 but very few records of feral populations exist until 2004 (Coutanceau 2006a), when the species started to spread across the country from the north, close to its probable introduction point in Belgium (Adriaens et al. 2003). Maps of first observations of *H. axyridis* at particular locations in France suggest a heterogeneous process of diffusion, with some regions rapidly colonized whereas in others there is a lag in invasion, or *H. axyridis* remains absent (see maps in http://vinc.ternois.pagesperso-orange.fr/cote_nature/Harmonia_axyridis). First observation records have been used in sophisticated modelling approaches to make inferences about the relative impact of various environmental and anthropogenic factors on that spread (Veran et al. 2015) and confirmed that the rate of colonization of *H. axyridis* in France was heterogeneous in time and space. Anthropogenic factors explained more variation of the diffusion process than environmental ones. The relative surface of urbanized area was the major anthropogenic factor increasing the probability of colonization. More specifically, low urban densities, corresponding to rural areas, represented unfavourable habitats. Finally, average summer temperature was the

main environmental factor affecting colonization, with negative impact for both high and low values.

IAS expanding their range provide unique opportunities to explore the effect of spatial spread on life-history traits, making it possible to test for a spatial arrangement of dispersal abilities along the expanding range (Phillips et al. 2007; Purse et al. 2014). Moreover, the question of the evolution of dispersal capacity in invasive populations is highly relevant, because it may accelerate spread, with serious applied and theoretical consequences (Phillips et al. 2010; Travis and Dytham 2002). Using controlled experiments in laboratory conditions, clear evidence was found of a strong, rapid increase in flight speed with range expansion of *H. axyridis* from the core of the invaded area in Western Europe (Belgium) to the front of this invaded area in South and Western parts of France (Lombaert et al. 2014). This shift towards a higher flying speed at the invasion front was remarkably rapid, as it was demonstrated after only 8 years of expansion, corresponding to about 16 generations (Koch 2003).

Using population genetic approaches, it has been shown that the *H. axyridis* sampled across France (see below for exceptions) belonged to a single genetic unit that has invaded the Western part of Europe (Lombaert et al. 2010, 2011). This invasive population bears traces of genetic admixture between an eastern North American wild source, which was found to have served as a “bridgehead source” for many worldwide invasive outbreaks, and a biological control strain used in Europe (Lombaert et al. 2010). Experimental studies in the laboratory have investigated the phenotypic impacts of such genetic admixture (Facon et al. 2011; Tayeh et al. 2012, 2013, 2015; Turgeon et al. 2011). Biological control individuals were found to display classic *r*-selected traits with a shorter lifespan and an earlier egg production when compared to native and US invasive individuals. European invasive individuals have shown phenotypic traces of the genetic admixture between US invasive and biological control individuals. For most traits (such as age at the start of reproduction, total adult and reproductive lifespan), European invasive individuals displayed intermediate values between both parents. Thus genetic admixture has had a long-lasting effect in the wild by shaping the life-history strategy of the European invasive individuals of *H. axyridis*. In France, and more generally Western Europe, the exact

role of admixture with the European biological control strain in the process of invasion remains poorly known. The single eastern North American origin of one South African and two South American outbreaks indicates that the genetic admixture observed in Western Europe is not required for an eastern North American propagule to establish and start an invasive population in diverse ecological contexts (Lombaert et al. 2014). It seems therefore unlikely that admixture in Western Europe has radically changed the outcome from failed to successful invasion. Such admixture has probably simply modulated the rate (or impact) of an invasion process that would have been successful anyway.

In addition to the single vast admixed population which invaded Western Europe, a genetically distinct population established in South East of France has been identified (Lombaert et al. 2014). This population was first observed in 2005, and it appeared to have originated exclusively from the European biological control strain introduced into Europe from 1982. This is surprising, at first sight, because European biological control individuals have long been thought to be unable to survive in the wild (Ferran et al. 1997). In support of this, it is apparent that this distinct population does not seem to have expanded spatially, unlike most of the other *H. axyridis* outbreaks known all over the world. This locally established population might attest, however, to the ability of the European biological control strain to found small overwintering populations in the wild, in areas with clement winters.

Germany

In 2000 the first German record of *H. axyridis* in the wild was reported from Frankfurt City in 2000. This was followed 2 years later by reports of *H. axyridis*, in higher abundance than the first records, from Frankfurt region and also Hamburg (Klausnitzer 2002). It has spread rapidly into other regions across Germany and is now considered established throughout Germany, although there has been no nation-wide monitoring to confirm this assumption. In south-west Germany near Frankfurt peak population densities were observed in early autumn until 2009 and also in 2012 but there seems to have been declines in numbers since then. However, this information is not derived from systematic monitoring.

Several German populations from 2008 to 2009 were examined for the presence of antagonistic microorganisms (bacteria, fungi, microsporidia) and invertebrate parasites (Herz and Kleespies 2012).

Italy

In Italy, *H. axyridis* was released in protected crops as a biological control agent from 1995 to 1999. However, the use of *H. axyridis* for biological control was suspended because concerns over adverse impacts became apparent. The first occurrence of establishment was in 2006 in Piedmont followed by subsequent observations in Emilia-Romagna in 2008 and rapid establishment in 16 out of 20 Italian regions with particularly widespread occurrences across northern and central Italy (Burgio et al. 2008b; Cornacchia and Nardi 2012). The origin of the populations is unknown; individuals could be either offspring of those released in situ or immigrants from other parts of Italy, France or Switzerland (Burgio et al. 2008b).

Research studies in Italy have focused on *H. axyridis* biology (Bazzocchi et al. 2004) and specifically life table parameters. Research on the occurrence of parasitoids attacking *H. axyridis* is ongoing (Francati 2015; Rondoni et al. 2013). Other studies are focusing on the development of a liver-based artificial diet, which could assist in maintenance of cultures of adult *H. axyridis* (Sighinolfi et al. 2008), and on the susceptibility of *H. axyridis* larvae to lambda-cyhalothrin insecticide (Benelli et al. 2015).

Norway

Harmonia axyridis was assessed as a potential biological control agent for use in Norwegian greenhouses in 2001 (Statens landbrukstilsyn 2001). It was concluded that *H. axyridis* might become established outdoors and thereby pose a risk to the environment. The assessment was therefore negative with respect to import and commercial use of *H. axyridis* in Norway.

The first record of *H. axyridis* in Norway was in Oslo in 2006, the adult female f. *succinea* arrived as a stowaway on horticultural plants, *Thuja* sp. (Cupressaceae) imported from the Netherlands to Norway (Staverløkk 2006). In late 2007 and throughout 2008 several adults were found indoors and outdoors at a number of locations in the urban and suburban areas of Oslo (Sæthre et al. 2010a, b).

Observations in areas some distance from Oslo, such as Tvedestrand in Aust-Agder County (2008), Våle in Vestfold County (2008) and Trondheim (2009; the latter about 600 km north of Oslo) revealed further spread or separate introduction to new areas (Sæthre et al. 2010a, b). Repeated introductions (probably on imported plants) are likely to be the most important factor for introduction of the species to new areas in Norway. Natural geographic barriers and long distances within Norway limit the species possibilities for rapid natural dispersal. However, anthropogenic spread facilitates dispersal and of particular note was the occurrence of between 2000 and 3000 adult *H. axyridis* in a cargo of timber imported to Åndalsnes (Møre og Romsdal County) in March 2008 from Pennsylvania, USA. Some specimens were also recorded at Snåsa (Nord-Trøndelag County) on the imported timber which was transported from Åndalsnes. According to the importing timber company, actions had been taken to eradicate the beetles.

In late 2008 a website was launched to engage the public in submitting observations on-line and this has made a major contribution to documenting the distribution of *H. axyridis* in Norway (Sæthre et al. 2010a, b). Records are available at <http://www.artsportalen.artsdatabanken.no/#/Harmonia+axyridis/7468>. In autumn 2015 high numbers of *H. axyridis* were reported from overwintering aggregations across the city of Oslo. However, so far, the distribution of *H. axyridis* in Norway appears to be limited to urban and suburban regions, and it has to date not been recorded or reported in commercial crops or in natural habitats. Further studies on the biology, ecology, cold tolerance and winter survival will contribute to better predictions of the dispersal and establishment potential of *H. axyridis* in Scandinavia.

Slovakia

Harmonia axyridis was first recorded in Slovakia in 2008 (Majzlan 2008). It arrived as an unintentional introduction by secondary spread, following the spread across Austria (Rabitsch and Schuh 2006), Poland (Przewozny et al. 2007) and the Czech Republic (Špryňar 2008). There was less than 1 year between the first record of establishment and widespread occurrence of *H. axyridis*. By the end of 2009, it was recorded across Slovakia, and by the end of 2012 it occurred in numerous habitats, particularly

gardens, orchards and urban areas. The records from 2008 to 2012 document the invasion clearly (Panigaj et al. 2014). The distribution and time sequence of the records support the maximum rate of the spread of *H. axyridis* to be approximately 200 km year^{-1} , the spread being accelerated by human movement (Panigaj et al. 2014). The local topography played a crucial role in the spread: 47 % of the records of the coccinellid were from lowlands (94–200 m), 36 % from low hilly areas (200–400 m), 11 % from moderate altitudes (400–600 m) and only 6 % from higher areas (600–1250 m a.s.l.; Panigaj et al. 2014). Despite great efforts in 2013 and 2014, only a single specimen of *H. axyridis* was recorded from altitudes above 1000 m.

Wildlife records in Slovakia are mostly shared through popular naturalist's web pages (e.g. www.nahuby.sk, www.fotonet.sk) which also provide information about *H. axyridis*. The Facebook page Lienky Slovenska (Ladybirds of Slovakia) was launched in 2015 to encourage the public to take part in ladybird surveys focusing on *H. axyridis*. The international cooperation with scientists and collaboration with volunteers within the Slovakia is critical for progress with further research on *H. axyridis*.

Switzerland

The first *H. axyridis* adult was found in 2004 in Basel, but it was only in 2006 that establishment was confirmed in several locations (Eschen et al. 2007). From then, the ladybird rapidly invaded all areas of low and middle altitudes within 2 years. A long-term inventory was initiated in the northwest of Switzerland in 2006 to record the impact of *H. axyridis* on native ladybirds (Eschen et al. 2007). Ladybird populations were monitored using standardised sampling methods at 45 sites: 15 broadleaved hedgerows, 15 meadows and 15 conifer sites several times a year. The monitoring was interrupted only in 2014 but has since restarted. Other surveys were made in other habitats on an irregular basis, in particular on urban trees. Since 2008, *H. axyridis* has become by far the most abundant ladybird on broad-leaved shrubs and trees, accounting for 60–80 % of all ladybirds collected throughout the year. In contrast, in meadows and on conifers, *H. axyridis* still remains rather uncommon, except on some specific plants such as nettle (Kenis and Eschen, unpublished data).

Further studies in Switzerland have also focused on the impact of *H. axyridis* on native ladybird populations. The occurrence of intraguild predation in the field using polymerase chain reaction (PCR) to identify target prey DNA within a predator's gut has been investigated (Aebi et al. 2011). IGP between *H. axyridis* and eleven native non-target European ladybirds in laboratory experiments has been studied (Katsanis 2011).

The Netherlands

Harmonia axyridis was first released as a biological control agent in greenhouses in 1995, on outdoor crops, arboriculture and in urban areas since 1996, largely for the control of aphid pests (Cuppen et al. 2004). Releases were stopped by the end of 2003. *Harmonia axyridis* has established at some sites very rapidly with the first report of *H. axyridis* in the wild in 2002 in Groesbeek, Gelderland (as a pupa on a leaf of *Hedera helix* L. (Araliaceae) (Cuppen et al. 2004) followed by a specimen in Rotterdam, South Holland in 2003, and around the same time another specimen was collected in Reimerswaal, Zeeland. In July 2003 the first adult *H. axyridis* was collected on a lighted white sheet at night at a nature reserve (De Kaaistoep, North Brabant; Cuppen et al. 2004; van Wielink and Spijkers 2013). In this locality, up to 2014, 6516 specimens have been collected using light, 71.9 % of which were males (yearly range between 65 and 80 %; van Wielink, unpublished data).

From 2004 onwards, numbers of *H. axyridis* started to rise dramatically and monitoring efforts were increased (via <http://www.knnv.nl>, <http://www.stippen.nl> and <http://www.waarneming.nl>). While up until 2004 (mainly) the south part of the country was invaded, by 2007 more than 2000 records had been received covering the entire country, including the Wadden Islands (Brown et al. 2008a). *Harmonia axyridis* is now widely distributed and the dominant ladybird species, predominantly on trees and shrubs but also on herbs in urban and anthropogenic habitats, it is less abundant in (semi-) natural areas such as heathland and grasslands. In agricultural areas *H. axyridis* is considered the dominant ladybird in corn, but not in cereals. During the early years of invasion, until 2010, local abundance was particularly high during early summer and autumn but this has not been so apparent in recent years.

Research in the Netherlands has focused on natural enemies (Haelewaters et al. 2012; Raak-van den Berg et al. 2014; Sloggett 2010) and the high overwintering survival of *H. axyridis* (70.8–88.2 %; Raak-van den Berg et al. 2012). The latter study found that overwintering survival was higher (1) at sheltered places compared to exposed sites and (2) when ladybirds were overwintering at south-western sides of buildings. As a comparison, winter survival of *A. bipunctata* in the Netherlands is 17–78 % (Brakefield 1985).

United Kingdom

The UK has a long history of involvement of volunteers in gathering information on wildlife through biological recording (Pocock et al. 2015; Roy et al. 2015a). The Coccinellidae Recording Scheme (hosted by the Biological Records Centre which is part of the Centre for Ecology & Hydrology) was established in 1971 (Roy et al. 2011a). The legacy of ladybird recording in the UK provided a unique dataset through which to explore the impacts of *H. axyridis* on other ladybirds. *Harmonia axyridis* arrived in Britain through dispersal and introduction events from regions (mainly Europe) in which it was deliberately released as a biological control agent (Brown et al. 2008b). *Harmonia axyridis* was first recorded in the UK in 2003 (Roy et al. 2012c) and was established by 2005. An on-line survey (www.ladybird-survey.org) was launched to monitor the spread of *H. axyridis* while promoting the continued recording of other ladybirds. Tens of thousands of people have provided records of *H. axyridis* and other species of ladybirds (Roy et al. 2015b), providing an invaluable large-scale and long-term dataset which has been used to explore the invasion process and concomitantly trends in the distribution of other ladybirds (Comont et al. 2012, 2014a; Purse et al. 2014; Roy et al. 2012b). For example, declines in the distribution of seven (of eight assessed) native species of ladybird have been demonstrated, and correlated with the arrival of *H. axyridis*, using the records collated through the UK Ladybird Survey (Roy et al. 2012b).

The rapid spread of *H. axyridis*—more than 100 km per year across the UK (Brown et al. 2008b)—has been attributed to its high natural dispersal capability through both flight (Jeffries et al. 2013; Lombaert et al. 2014; Maes et al. 2014) and anthropogenic transport (Brown

et al. 2011b). A number of factors are considered to have contributed to the successful establishment and dominance of this polymorphic species within aphidophagous guilds across the UK, including high reproductive capacity, intra-guild predation, eurytopic nature and high resistance to natural enemies within the invaded range (Roy and Brown 2015).

Considerable attention has been given to experimental research (Comont et al. 2014b) and systematic field surveys (Brown et al. 2011a) to further understanding of the interactions between *H. axyridis* and other species. Future work will reflect the opportunities presented by *H. axyridis* to explore the complex and dynamic role of natural enemy interactions in the invasion process through community (network) approaches (Roy and Lawson Handley 2012). The role of citizen scientists in gathering information on species interactions is considered an important component of this research.

Africa

In North Africa, *H. axyridis* was introduced for biological control use in Tunisia around 1990 and in Egypt before 2000 (El-Arnaouty et al. 2000). It is thought to be established in limited areas of the latter, but not the former (Brown et al. 2011b).

According to unpublished records and misplaced voucher specimens discovered only in mid-2015, *H. axyridis* was intentionally released in South Africa around 1980 (Stals unpublished). This contradicts the previously published view that the species had never been intentionally introduced to this country (Stals and Prinsloo 2007; Stals 2010). The beetles were sourced from the USA, apparently originating from Japan. The release was made in an attempt to control the black pine aphid, *Cinara cronartii* Tissot & Pepper, in the Sabie area, in the present-day Mpumalanga Province. In the newly found records, a later, but undated, entry notes that the species had not established. No other information is presently available. It seems probable that this release failed, since no specimens of *H. axyridis* collected in southern Africa before 2001 are present in any public insect collection in South Africa.

Unaware of the above, Stals and Prinsloo (2007) announced that *H. axyridis* was first recorded in South Africa in 2004, in the Western Cape Province. However, museum records later revealed that adults

and immature stages had been found in the Cape Town area as early as 2001 (Stals 2010). This remains the earliest known date and location of establishment in southern Africa. Sabie, the 1980s release point, is c. 1800 km away from Cape Town. *Harmonia axyridis* specimens from the Sabie area were only recorded in the austral summer of 2008 (Stals unpublished), when the contemporary spread of the invader into Mpumalanga was already well underway (Stals 2010).

The introduction pathway of the contemporary invaders in South Africa is unknown, but all analysed South African populations originated from eastern North America (Lombaert et al. 2010, 2014). Introduction was likely unintentional, but it is unknown whether there was more than one introduction to South Africa, disregarding the almost certainly failed introduction of the 1980s.

The only coordinated data-gathering initiatives for insects in South Africa are for Lepidoptera and Neuroptera. Nonetheless, recording of the range expansion through southern Africa mainly depends upon volunteer contributions. Until 2010, contributions were encouraged through sustained calls in popular media (Stals 2008, 2010). Since 2011, the citizen science web application iSpot (Silvertown et al. 2015) has been exploited as a recording platform for southern Africa and became the source of many high-quality observations of *H. axyridis*. An expert Coleoptera taxonomist assesses all contributions, querying contributors where necessary.

Harmonia axyridis rapidly spread widely through much of South Africa (Stals 2010; unpublished). It seems established largely in cooler and more mesic parts of the country, viz. the south-western, southern and interior-eastern Cape regions, and the more northern eastern and east-central areas, with few records from the semi-arid western and west-central reaches or the hot northern regions. No records have as yet come from the subtropical eastern coastal belt. The invader is well established and commonly encountered in the Fynbos and Grassland Biomes; established and not infrequently encountered in the Savanna Biome; but infrequently reported from other biomes. In South Africa, the majority of records come from urban and rural gardens or dwellings, and from agricultural land. Other southern African countries with records of *H. axyridis* are Lesotho (first record June 2008, Stals 2010) and Swaziland (first record November 2013, Stals unpublished), and the ladybird has likely established in both these countries.

In the rest of sub-Saharan Africa, *H. axyridis* has only been recorded in Kenya (Nedvěd et al. 2011) and Tanzania (Nedvěd and Háva 2016). In Kenya, a population was discovered in December 2010 at a coastal holiday centre and may represent an established population (Nedvěd et al. 2011). In Tanzania, only two *H. axyridis* individuals were found at a beach resort in Zanzibar in April 2014 and may represent a transient introduction with no establishment. These occurrences suggest that the invasion of tropical Africa is possible. The origin of the beetles in East Africa has not yet been investigated and all examined specimens were of the f. *succinea*.

Research on *H. axyridis* in South Africa is scarce but it is recognised that there is a need to assess its biology and ecology in order to evaluate its impact on native communities and agroecosystems. Researchers from the Centre for Invasion Biology, Stellenbosch University, are focusing on the thermal biology and life history of *H. axyridis* in South Africa and compare this species' traits to those of native aphidophagous ladybirds. This information can highlight characteristics that promote the invasiveness of *H. axyridis* in southern Africa and provide data for modelling its potential spread within and beyond borders (Shinner 2014). The study of its behavioural responses and adaptation to climate variation will remain a focus in the years to come as well as modes and mechanisms of introduction and range expansion investigated using molecular techniques.

However, many research aspects that are key for evaluating the establishment, spread and impact of *H. axyridis* are lacking. No systematic field surveys are taking place and therefore the invader's abundance across habitat types is also unknown. More importantly, data on the native ladybird communities (species richness and abundance) occurring in areas with and without *H. axyridis* are not being collected and the impacts on these communities are thus unknown. Of overriding importance may be the complete lack of baseline data prior to this invasion; it is possible that no readily comparable and uninvaded habitats may remain for urgent collection of baseline information. In addition, the taxonomy and phylogeny of the native Coccinellini need to be examined, in particular those African species currently placed in the genus *Harmonia*.

Under South African national legislation, *H. axyridis* is a Category 1b Listed Invasive Species

(Department of Environmental Affairs South Africa 2014a), which in terms of the National Environmental Management: Biodiversity Act, 2004, legally is a "species which must be controlled" (Department of Environmental Affairs South Africa 2014b). How such control is to be achieved is unclear at present.

Failure of *Harmonia axyridis* to establish in some regions

Harmonia axyridis is much more commonly and widely distributed in the northern than in the southern hemisphere, perhaps unsurprising given its Asian origin. While *H. axyridis* distribution extends to boreal regions in its native range, its invasive distribution in the north and south of Europe, and also in northern Canada and Alaska, is more limited and suggests that climatic factors may be important in limiting the spread of this species. Globally, there are very few records from tropical regions (23.4°N–23.4°S); where it has been reported from the tropics it is not widely spread (e.g., Colombia, Venezuela, Kenya, Tanzania). In both South America and Africa, limits to its distribution apparently include warm tropical but also arid environments.

In Europe there are some habitats and regions that appear to be resistant to the establishment of *H. axyridis*. Some examples are the limited evidence of establishment in Greece (Kontodimas et al. 2008), Turkey (Bukejs and Telnov 2015), Spain, including the Canary Islands (Goldarazena and Calvo 2007; Jacas et al. 2006; Pons et al. 2015), Bosnia and Herzegovina (Kulijer 2010), Portugal, including the Madeira and Azores archipelagos (Garcia 1986; Soares et al. 2008), Northern Ireland (Murchie et al. 2008), the Republic of Ireland (<http://www.invasivespeciesireland.com>), and Réunion (Quilici, personal communication). It is as important to consider the regions in which *H. axyridis* has failed to establish as those in which it has succeeded. Only recently has consideration been given to understanding invasion failures within the context of invasion processes (Zenni and Nuñez 2013). The factors limiting invasion by *H. axyridis* in some geographic areas are worthy of exploration and could potentially provide insights into whether the southern and northern European ecosystems are more resilient to invasion than other parts of Europe and beyond. Investigation

of equivalent patterns on the southern African sub-continent would also be informative.

Records of successful breeding by *H. axyridis* are very limited in Scotland (Roy and Brown 2015) and although climatic conditions are not thought to have been a barrier to the colonization and spread of *H. axyridis* in southern Britain, it is possible that climate has limited its abundance not only in northern England and Scotland (Brown et al. 2008b; Roy and Brown 2015), but also Denmark (Steenberg and Harding 2009b) and further north throughout Scandinavia. The combination of lower temperatures and higher precipitation in Scotland compared to England could be limiting the distribution of *H. axyridis* within Scotland. The Orkney and Shetland Islands are considered climatically unsuitable for *H. axyridis* (Poutsma et al. 2008), and in support of this there have only been occasional records of adults, arriving on produce imported from the mainland, from these northern islands (Ribbands et al. 2009). There are no records of immature stages of *H. axyridis*, or other ladybird species, on these islands.

Although thousands of individuals of both f. *succinea* and f. *conspicua* have been released in the Azores (Garcia 1986; Schanderl et al. 1992), *H. axyridis* has not become established there (Evans et al. 2011; Soares et al. 2008). It has been hypothesised that prey features related to local plant habitats and landscape structure, together with the ladybird characteristics in terms of body size, might explain why the invader is absent (Hemptinne et al. 2012). The coastal terrestrial habitats that form 9 % of the landscape are the richest in terms of food resources for aphidophagous ladybirds. It is predicted that other large and medium-sized species of ladybirds (*Coccinella undecimpunctata* L.), which have requirement for high prey consumption, will also decline because of shortage of prey (Borges et al. 2006; Cabral et al. 2006; Sebastião et al. 2015; Soares et al. 2001) for example *C. septempunctata* is considered extinct from the Azores. The Azorean communities are nowadays dominated by minute Scymnini species and larger species are no longer recorded. Despite the competitive advantage of *H. axyridis* against the native *C. undecimpunctata* (Felix and Soares 2004; Nória et al. 2008), it is apparent that Azorean habitat characteristics and the high feeding rate of *H. axyridis* are hampering its invasion.

Comparison of traits

There have been a number of studies examining the influence of life-history traits on invasion and *H. axyridis* is no exception (Comont et al. 2012, 2014a). The traits databases compiled for these studies provide a rare opportunity to explore variation in life-history traits between localities (native and invaded) around the world. Extending and combining traits databases to a global scale will provide intriguing insights. The invasion process and ecological attributes (Table 1) and the compilation of life history traits of *H. axyridis* (Table 2) represent the start of this process and highlight gaps in understanding. However, qualitative comparisons of the traits of *H. axyridis* across the invaded range and with the native range reveal patterns that are worthy of further investigation.

Habitat

The habitat of *H. axyridis* is wide and although poorly documented in many regions the exploitative and opportunistic nature of this species is evident (Table 1). During early stages of invasion it has been noted that *H. axyridis* is more prevalent within urban and agricultural landscapes than in semi-natural landscapes (Brown et al. 2008b; Grez et al. 2014a, b). *Harmonia axyridis* is common within gardens and parks throughout the year and its presence in agricultural fields, orchards or vineyards has been documented globally and local damage due to quality loss of fruits is known (Koch et al. 2004a). Across Europe and Japan *H. axyridis* is commonly associated with trees and shrubs. For example in urban areas in Europe it is the most abundant ladybird on lime (*Tilia* spp.) and maple trees (*Acer* spp.) but is also frequently found on Scots pine, *Pinus sylvestris* L. (Pinaceae). The habitats of *H. axyridis* in Japan are disturbed areas such as agricultural fields, orchards, parks, residential yards and gardens (Osawa 2011) and *H. axyridis* is generally uncommon in natural forests (Osawa 2011).

In winter *H. axyridis* has a propensity to aggregate in buildings. Across Europe adults usually start aggregating in October and leave overwintering sites in April. The aggregating behaviour has been shown to depend on two blends of long chain hydrocarbon molecules, one leading conspecifics towards aggregation sites and the other ensuring cohesion of the

Table 2 Life history traits of *Harmonia axyridis* documented from countries around the world

	Body size	Colour form(s)	Voltinism	Fecundity	Hatching success	Temperature tolerance and development
China	Egg: length 1.0–1.5 mm 4th larval instar: length 10–15 mm Pupa: length 7 mm, width 4 mm Adult: length 5.4–8.0 mm, width 3.8–5.2 mm	>200 colour forms including: <i>succinea</i> <i>spectabilis</i> <i>conspicua</i> <i>axyridis</i>	2–8	Clutch size: 29.95 ± 0.46 (mean ± SD) Lifetime: 1063.02 ± 62.15 (mean ± SD)	84.85 ± 0.46 %	Development threshold: 10.5 °C; cannot develop above 34 °C Accumulated temperature: 231.3 degree-days
Japan	Egg: volume 0.25 ± 0.04 µl (mean ± SD) Adult female: size 6.73 ± 0.53 mm (n = 1106, mean ± SD) Adult male: size 6.16 ± 0.43 mm (n = 813)	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i> <i>axyridis</i>	2–3	Clutch size: 39.11 ± 1.47 Lifetime: 455.4 ± 163.46	65.84 ± 4.34 % (including individuals with male-killing endosymbiont)	Not measured
Siberia and the Far East	4th larval instar: length 8.2–11.2 mm Adult length: 4.9–8.2 mm	In population living west to Baikal lake almost all specimens are <i>axyridis</i> ; other forms are rare. In populations living east to Baikal lake 3 colour forms are common: <i>succinea</i> <i>conspicua</i> <i>spectabilis</i> Other forms are rare	1–3	Clutch size: 11–52	Not measured	Mating at 16–18 °C. Optimal temperature for egg development: 17–26 °C; for larval development: 26–30 °C; for pupal development: 22–30 °C All stages can survive at temperature 40 °C for several hours
European Russia	Not measured	4 colour forms: <i>succinea</i> <i>spectabilis</i> <i>conspicua</i> <i>axyridis</i> Populations in the vicinity of Sochi and Abkhazia are all <i>succinea</i>	At least 2	Not measured	Not measured	Not measured

Table 2 continued

	Body size	Colour form(s)	Voltinism	Fecundity	Hatching success	Temperature tolerance and development
USA and Canada	Adult: length 4.8–7.47 mm, width 3.9–5.89 mm Egg: 0.25 ± 0.0 mg Adult male: 31.6 ± 0.9 mg Adult female: 53.6 ± 2.2 mg	Mainly <i>succinea</i> ; melanica <i>H. axyridis</i> uncommon	2 plus a partial third	Clutch size: single eggs to more than 20 per cluster (> 60 % of 3149 females observed had egg cluster with > than 20 eggs) 37.3 ± 4.3 eggs per day	93.6 % non-cannibalising larvae and 94.1 % of larvae that had engaged in sibling cannibalism survived to adulthood (laboratory) In wild-caught individuals 97 ± 4 % (n = 22 egg clutches)	Development from egg to adult requires 231.3 degree days above a lower developmental threshold of 10.5 °C
Chile	Larvae: length L1: 1.96 ± 0.04 mm; L2: 4.6 ± 0.08 mm; L3: 6.3 ± 0.11 mm; L4: 8.3 ± 0.17 mm Adults female: length 7.2 ± 0.04 mm (range 6–8.3 mm); width 5.6 ± 0.06 mm (range 4.7–6.2 mm) Adult male: length 6.7 ± 0.04 mm (range 5.5–7.7 mm), width 5.3 ± 0.05 mm (range 4.1–5.8 mm)	<i>succinea</i> with some variation in spot number and red intensity	2–3	Clutch size: 14.1 ± 1.2 eggs per day at 20 °C (fed with <i>A. pisum</i>)	Not measured	No study of tolerance but in relation to preference <i>H. axyridis</i> preferred temperatures between 15 and 20 °C, with thermal range between 8.6–27.2 °C. No eggs hatched at 33 °C
Belgium	Adult: length 5–9 mm (median = 7)	<i>succinea spectabilis conspicua</i>	2 in (semi-) natural areas, one in field crops (second develops late in the season in other habitats)	Clutch size: 12–48 eggs (depending on food source and colour morph)	15–64 % (depending on food source and colour morph)	Lower lethal temperature for outdoor overwintering: from –17.1 to –16.3 °C Lower lethal time of field populations at 0 and –5 °C: 18–24 and 17–22 weeks respectively

Table 2 continued

	Body size	Colour form(s)	Volinism	Fecundity	Hatching success	Temperature tolerance and development
Czech Republic	Adult female: (reproduction period) 44.3 ± 9.3 mg; (migrating) 36.1 ± 5.7 mg Adult male: (reproduction period) 29.8 ± 6.0 mg; (migrating) males: 30.0 ± 5.3 mg Not measured	88 % <i>succinea</i> 9 % <i>spectabilis</i> 3 % <i>conspicua</i> <i>axyridis</i> —rare <i>equicolor</i> —extremely rare	2–3	Clutch size: 21 eggs per day (max. 86) Lifetime: 1174 eggs (max. 2497)	82 %	High egg and larval mortality at 33 °C; LDT 11 °C, SET 175 DD
Denmark	Not measured	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i> <i>axyridis</i>	2 plus occasional partial third	Not measured	Not measured	Not measured
France	Adult female: length 7.19 ± 0.18 mm; width 5.71 ± 0.11 mm; mass 51.5 ± 5.5 mg Adult male: length 6.55 ± 0.11 mm; width 5.40 ± 0.09 mm; mass 40.2 ± 3.9 mg	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i>	2–3	Clutch size: 33.5 ± 5 eggs (at 24 °C, 60 % RH, L:D 14:10; fed ad libitum with irradiated eggs of <i>E. kuehniella</i>)	79.5 ± 12.8 %	Not measured
Germany	Adult female: length 5.8 ± 0.4 mm; width 4.2 ± 0.3 mm Adult male: length 5.4 ± 0.4 mm; width 4.0 ± 0.3 mm	92 % <i>succinea</i> 7 % <i>spectabilis</i> 1 % <i>conspicua</i>	2	Not measured	Not measured	Not measured
Italy	Adult female: length 7.14 ± 0.10 mm; width 5.54 ± 0.07 mm (n = 24) Adult male: length 6.48 ± 0.08 mm; width 5.19 ± 0.07 mm (n = 20)	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i>	At least 2, potentially 4	Clutch size: 15.4 ± 3.9 eggs Lifetime: 560.5–783.8 eggs 228.3 ± 30.7 eggs laid in 10 days	58–100 % (n = 988) reared on <i>Aphis fabae</i> ; 53 % reared on <i>M. persicae</i>	At 35 °C: no egg hatching At 30 °C: 12.8 ± 0.19 d preimaginal development time; 1.15 ± 1.01 egg fertility (%) At 25 °C: 13.84 ± 0.09 d preimaginal development time; 21.63 ± 5.12 egg fertility (%)

Table 2 continued

	Body size	Colour form(s)	Voltinism	Fecundity	Hatching success	Temperature tolerance and development
The Netherlands	Adult: length 5.4–7.8 mm (median = 6.8); H/L elytra 0.44–0.48 mm Adult female: 28.2–37.9 mg Adult male: 24.1–32.8 mg	81 % <i>succinea</i> 16 % <i>spectabilis</i> 4 % <i>conspicua</i> <i>axyridis</i> (6 records) <i>equicolor</i> (6 records) very sporadically (less than 1:1000) <i>intermedia</i>	2–3	Clutch size: 20–30 eggs	Not measured	Nightly flight activity commences at 10.5 °C
Norway	Not measured	<i>succinea</i>	Not measured, suggests 1–2	Not measured	Not measured	Not measured
Slovakia	Adult female: length 6.0–7.5 mm (median = 6.8 mm); width 4.7–5.9 mm (median 5.4 mm, n = 38) Adult male: length 5.8–7.0 mm (median 6.5 mm); width 4.1–5.9 mm (median 5.1 mm, n = 34)	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i> <i>axyridis</i> <i>equicolor</i>	2	Not measured	Not measured	Not measured
Switzerland	Not measured	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i>	2 (in Northern Switzerland, measured by regular sampling programmes)	Not measured	Not measured	Not measured
UK	Adult female: length 5.8–8.0 mm (median = 7.0); width 4.8–6.5 mm (median = 5.4, n = 37) Adult male: length 5.4–7.5 mm (median = 6.7); width 4.6–5.9 mm (median = 5.1, n = 39)	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i>	2 (but with occasional partial third generation)	Not measured	Not measured	Not measured but UK distribution currently limited within Scotland and climatic factors (particularly temperature) assumed to be important

Table 2 continued

	Body size	Colour form(s)	Volitinism	Fecundity	Hatching success	Temperature tolerance and development
South Africa	Adult female: length 6.9 ± 0.1 mm (n = 10); mass 35.3 ± 1.0 mg (n = 34) Adult male: length 6.3 ± 0.1 mm (n = 10); mass 29.1 ± 0.9 mg (n = 31)	<i>succinea</i> with variation in spot number and background colour	Exact number unknown but at least 2	Over 70 days: 245 ± 40 eggs Rearing conditions: 25/18 °C (18 h day/6 h night cycle; 14hL/10hD photoperiod)	53 ± 6.5 % (n = 650) Rearing conditions: 25/18 °C (18 h day/6 h night cycle; 14hL/10hD photoperiod)	Development time: 23.1 ± 0.1 days (n = 267); CTmax = 44.1 ± 0.1 °C (n = 34); CTmin = 0.9 ± 0.2 °C (n = 31), start temp 25 °C, rate of change: 0.05 °C min ⁻¹ ; Rearing conditions: 25/18 °C (18 h day/6 h night cycle; 14hL/10hD photoperiod)

It is important to note that there are various measurements for some of the life history traits and so direct comparison between countries is not always possible. Standard approaches to capturing this information would be useful to enable quantitative assessments on a global scale. Body size has been measured either as length and/or width (mm) or volume (µl) or mass (mg). Volitinism is given as number of generations per year. Fecundity has been measured as clutch size (number of eggs per cluster) and lifetime (number of eggs per lifetime). In some cases the maximum (max.) number of eggs within a cluster is given. Hatching success is given as %. Temperature tolerance is measured in various ways: development threshold (°C), accumulated temperature (degree-days), lower lethal temperature (°C), lower lethal time (weeks), development time (days), maximum and minimum critical temperature (CTmax and CTmin respectively; °C). Unless otherwise stated mean ± standard error are given for all traits

aggregations (Durieux et al. 2012). These findings, with the identification of a volatile sex pheromone in female *H. axyridis* (Verheggen et al. 2007), might offer some potential in the development of specific control methods for *H. axyridis*.

It is critical that we have a better understanding of the habitat preference and suitability of *H. axyridis*; this is especially relevant when facing current global environmental change, especially urbanization, agricultural intensification and climate change which will undoubtedly affect the spread and distribution of *H. axyridis*. Habitat suitability could be estimated using Species Distribution Models based on fine-scale records on the presence/absence or densities of *H. axyridis* populations. Such results would have wide relevance to invasion biology.

Diet breadth

The wide diet breadth of *H. axyridis* is evident from Table 1 and, as already stated, includes pest and non-pest insects but also fruits. Perhaps of most interest and relevance to understanding the threat posed by this species to biodiversity, is the range of non-pest insects consumed and associated population-level effects. Much research has focussed on interactions between *H. axyridis* and other coccinellids (Pell et al. 2008) but there is a need for further work on other taxonomic groups for example expanding the research on butterflies such as the studies on the monarch butterfly *Danaus plexippus* (L.) (Koch et al. 2003, 2006a). Furthermore it is critical that future research considers the population-level effects of *H. axyridis* on different species and implications for ecosystem function. Current studies have not clearly documented the diet preference, adaptability and feeding efficiency of *H. axyridis*, which are essential for assessing its potential impact in recipient ecosystems.

Thermal tolerance

Only a few studies, representing populations of *H. axyridis* from a few regions, have considered thermal tolerance (Table 2; Koch et al. 2004b). Of particular importance would be to measure lower and upper temperature tolerance of several life stages using ecologically relevant conditions for the population examined. Indeed to build Species Distribution Models, thermal tolerance needs to be carefully

measured in the laboratory so that the reaction norm of physiological/behavioural performance as a function of ambient temperature can be established. However, *H. axyridis* usually overwinters in shelters and aggregations and cold tolerance measurements should be interpreted in regards to ecologically relevant conditions. Indeed *H. axyridis* can be found at a range of altitudes: in Chile individuals have been found at >3000 m a.s.l. while in central Europe it is regularly present from the eastern lowlands (114 m a.s.l.) to montane/subalpine forests (approx. 1600 m a.s.l., unpubl. data) in the Alps, with one isolated record of a probable wind-drifted individual at 2280 m a.s.l. in Carinthia.

Although laboratory studies show that invasive populations of *H. axyridis* do not survive at 34 °C (Benelli et al. 2015), the species has been documented in Kenya (Nedvěd et al. 2011) and Tanzania (Nedvěd and Háva 2016) but there is no evidence that this species is abundant in the tropics. In addition, the wide spread and occurrence of *H. axyridis* in mesic cool climates or pockets of urban gardens within drier environments in its novel range suggests that climatic factors other than temperature also play a role in shaping its distribution.

Desiccation resistance (Nedved and Kalushkov 2011) and the potential cross-effects of temperature and humidity on temperature limits may provide useful information for modelling its future distribution in face of climate change (Hoffmann et al. 2013). Perhaps more importantly, the study of the plasticity and evolutionary adaptation of tolerance limits in *H. axyridis* using both native and invasive populations would provide insights into its adaptive capacity to future climatic challenges. The effect of different climate regimes on the body weight and fat body content of *H. axyridis* and *C. septempunctata* has been the focus of laboratory studies in Germany (Krengel et al. 2012). This study concluded that that *C. septempunctata* has life history adaptations that would confer an advantage over *H. axyridis* at elevated temperatures.

Reproductive potential

A number of traits (voltinism, fecundity and egg hatching success) reveal the high reproductive potential of *H. axyridis* (Table 2). In the native range, *H. axyridis* is generally considered to have two

generations per year, although it can have three and occasionally up to eight generations in some years and localities (Osawa 2011). In Kyoto, in the centre of Japan, the overwintering adults mate and lay eggs in spring (Osawa 2000). The adults of the first generation emerge in mid May to June (Osawa 2000). In mid summer, the beetles aestivate in small groups in leaf-shelters on trees and the behaviour is regarded to be an adaptation to high temperature (Toda and Sakuratani 2006). In autumn, *H. axyridis* adults fly towards overwintering sites, white or pale objects on hilltops or valleys, where they aggregate from early November (Obata 1986).

Within much of the invaded range, *H. axyridis* only achieves two generations per year, whereas in the native range up to eight generations have been observed. Increases in global temperatures could facilitate an increase in voltinism, and corresponding increase in abundance across the invaded range in the future. On the contrary, increase in temperatures may limit its reproduction due to the high egg mortality observed at temperatures above 30 °C (Table 2).

We suggest that the three traits related to population demography and thus invasiveness, namely voltinism, fecundity and hatching success, need to be recorded in a standardised unit so that population dynamics can be estimated from matrix population models. Furthermore, the trade-offs between, and rates of adaptation in, life-history traits are of intrinsic theoretical value (e.g. the trade-off between these three demographic traits among populations in different environments) and colour polymorphism of *H. axyridis* (Table 2) is also an interesting model system in population genetics. Overall, we suggest that the strength of biotic interactions centralised around *H. axyridis* (i.e. diet preference and foraging efficiency) and the three demographic traits are key variables for monitoring/assessing its performance and impact in invaded ecosystems.

The reproduction success of individual females has been measured in variable ways in *H. axyridis* according to regions (Table 2). Usually reproduction is measured as lifetime fecundity (total number of eggs laid by female), but this requires very long breeding and observation, since many females of *H. axyridis* live and reproduce for over 4 months (Awad et al. 2013). Alternatively, fecundity during the first month of reproduction (beginning by the day of the first egg

laying, not including pre-oviposition period) is used. Both measures require feeding the females ad libitum with a suitable prey. Widely used types of prey that may become a standard are the pea aphid *Acyrtosiphon pisum* (Harris) (Hemiptera: Aphididae) and frozen eggs of the flour moth *Ephesia kuehniella* (Zeller) (Berkvens et al. 2010a; Kögel et al. 2012). Other measures of reproductive performance could include daily fecundity (after a standard time period for example 2 weeks after the start of egg laying) and cluster size (again after a standard time period and perhaps an average over 2 weeks).

Fertility is defined as the product of fecundity and hatching rate. Hatching rate (percentage of eggs that hatch to the first larval instar) should be calculated over the first month of reproduction, since it declines strongly later (Awad et al. 2013). Hatching rate in *H. axyridis* in different countries varied from 15 % in Belgium (Berkvens et al. 2008) to 100 % in Italy (unpublished data), although it has not been measured in most countries (Table 2). Hatching success may depend on many factors for example food source, colour morph, endosymbionts and multiple fertilisation. Thus permanent presence of one or more males with each female is recommended.

Colour forms

More than 200 colour patterns of *H. axyridis* elytra have been observed in the native range (China), but most of them can be categorized into four major colour forms (Du and Chen 2010; Tang et al. 2012). Controlled crossing experiments have shown that the majority of color patterns are controlled by 15 alleles at one locus with multiple alleles (Komai 1956). However, all but four of these alleles are rare in natural populations, with a combined frequency of less than one per cent. The four major alleles are *succinea*, *axyridis*, *conspicua*, *spectabilis*, all but the first of these being melanic forms (Michie et al. 2010): (1) yellow to red background colour of elytra with the number of black dots ranging from 0 to 19 (f. *succinea*); (2) black background colour of elytra with many orange-red dots (of varying size and position; f. *axyridis*); (3) black background of elytra with one large orange-red dot in the top-centre of each elytron (f. *conspicua*); (4) black background colour of elytra with two orange-red dots on each elytron and the top

one larger than the bottom one (f. *spectabilis*). The impressive diversity of colour patterns documented in China has been attributed to the diverse environmental conditions in the region as well as to complex interaction between rare allelic forms (Tan 1946). A hierarchical dominance with respect to phenotype expression was demonstrated between the four major colour alleles: *conspicua* > *spectabilis* > *axyridis* > *succinea* (Michie et al. 2010; Tan and Li 1934; Tan 1946). More specifically, the expression of the colour pattern in the heterozygous individuals (i.e. individuals bearing two different allelic forms) conforms to the rule of mosaic dominance heredity, which states that any portion of the elytra which has black pigment in the homozygote for a given allele will have black pigment also in the heterozygotes in which that allele is present (Tan 1946). Interestingly, Michie et al. (2010) reported that the non-melanic morph *succinea* dramatically increases its degree of melanization at cold temperatures, and that there is genetic variation in reaction norms, with different families responding to temperature in different ways. The exact genomic architecture and gene content of the multiallelic locus controlling color morph variation and phenotypic plasticity of the non-melanic morph remains unknown.

In some of the earliest research in population genetics, the frequencies of these alleles were found to vary hugely across the native range of *H. axyridis* (Dobzhansky 1933). The geographical variation appeared to be linked to climate, with the non-melanic form *succinea* being found most often in hot, arid regions and melanic forms being more frequent in cooler, more humid ones (Dobzhansky 1933). This might be considered as a consequence of climatic adaptation. However, a different pattern was found in Japan, where *succinea* decreases in frequency from northeast to south-west without any significant correlation to temperature or other climatic factors (Komai 1956). Moreover, in north China f. *succinea* dominates, whereas in south China the melanic colour forms dominate (Du and Chen 2010; Tang et al. 2012). In addition to this geographic variation, small to large seasonal changes in allele frequencies have been reported in some native populations (Jiang et al. 2007; Osawa and Nishida 1992; Tang et al. 2012). For example, in Beijing over half the population is melanic in the spring, but this drops to less than one-fifth by the autumn. Therefore, the melanic individuals

presumably have a large fitness advantage in the winter and a disadvantage in the summer. This has been attributed to the effects of thermal melanism, with melanism being costly in summer and beneficial in winter, possibly mediated by mate choice (Wang et al. 2009).

The range of colour forms is limited within the invaded range. Indeed in most invaded regions only the non-melanic morph f. *succinea* is present, except in Europe where the melanic morphs f. *conspicua* and *spectabilis* are also present (and rarely f. *axyridis*), probably due to the genetic admixture with European biological control strains which occurred in this region (Lombaert et al. 2010, 2014). So far, it is not possible to say whether the predominance of f. *succinea* observed in the invaded range is due to historical and/or demographical contingencies (i.e. simple random effects) or to any selective process that would have favoured the establishment and the spatial spreading of f. *succinea*, for example the phenotypic plasticity of this morph (Michie et al. 2010). Geographical and seasonal variation of melanic and non-melanic morphs remains rather sparsely studied in Europe (Purse et al. 2014). In Belgium, the initial point of introduction of the species, the most commonly encountered morph is f. *succinea*, and the proportion of melanics (f. *spectabilis*, f. *conspicua*) is about 25 % (Adriaens et al. 2008). In this particular region of Europe, strong cold hardiness and differences in several fitness parameters between melanics and non-melanics from field populations have been demonstrated (Berkvens et al. 2008, 2010a).

Natural enemies

Many regional reports have been published about one or several natural enemies of *H. axyridis* both within the native and invaded range but much could be revealed from a systematic approach comparing the native and invaded range (Table 1). There are a number of theories relating to IAS and their interactions with natural enemies but perhaps the most widely known is the Enemy Release Hypothesis (ERH; Jeffries and Lawton 1984; Roy et al. 2011b; Roy and Lawson Handley 2012). The ERH predicts that an alien species introduced to a new region will increase in distribution and abundance because of reduced impacts from natural enemies. Adopting a ‘biogeographical’ (compare richness and impacts of enemies

in native and introduced populations of an alien host) or ‘community’ (compare native and alien species occurring within the same community) approach for *H. axyridis* would be informative (Colautti et al. 2004). With both ‘biogeographical’ and ‘community’ approaches it is essential to consider how the loss of enemy diversity translates into population regulation. A small number of enemies may have large effects and so functional diversity of enemies may be a better predictor of impacts upon hosts than overall diversity. There is considerable scope for global collaboration in exploring *H. axyridis* within the context of ERH.

Generalist predators do attack ladybirds, for example sparrows have been confirmed as predators of *H. axyridis* in Slovakia (Veselý et al. *in press*), but parasites are the dominant natural enemies of ladybirds. Ladybirds are attacked by over 100 species of hymenopteran and dipteran parasitoids and several fungi (Ceryngier et al. 2012; Herz and Kleespies 2012; Riddick et al. 2009). Of these, the majority of research globally has focused on the parasitoid *Dinocampus coccinellae* (Schrank; Hymenoptera: Braconidae), which attacks both native and alien ladybirds (Ceryngier et al. 2012). *Dinocampus coccinellae* is a parasitoid of ladybirds that has a global distribution (Ceryngier et al. 2012) but currently the influence of alien ladybirds on the abundance and distribution of this parasitoid is unknown. Ladybirds vary in their quality as a host (Comont et al. 2014b; Koyama and Majerus 2008), but *D. coccinellae* does not discriminate between suitable and unsuitable ladybirds and will attack individuals differentially based on colour and movement (Cartwright et al. 1982; Obrycki et al. 1998; Richardson and Deloach 1972). Thus, the presence of unsuitable alien ladybird hosts such as *H. axyridis* may function as an ecological trap for the parasitoid, with positive effects on native ladybirds, or alternatively increase the abundance of the parasitoid, with adverse consequences for native ladybirds. It is apparent that *H. axyridis* is less susceptible to *D. coccinellae* than are other ladybirds (Berkvens et al. 2010b; Comont et al. 2014b) but it seems to be the most abundant and frequent *H. axyridis* parasitoid in many countries (Table 1; Francati 2015). Ongoing work is exploring the differences in immune response between *H. axyridis* and other ladybirds (Murray et al. 2015).

A semi-field study from the UK confirmed low rates of parasitism of *H. axyridis* by parasitoids, particularly

in comparison to the native *C. septempunctata* (Comont et al. 2014b). Pupae of *H. axyridis* were parasitized, primarily by *Phalacrotophora fasciata* (Fuller) and *Phalacrotophora berlinensis* Schmitz (Diptera: Phoridae), at an exceptionally low level (1.73 %) and adults were not found to be parasitized at all in this study; parasitism of the co-occurring *C. septempunctata* was high (20.91 % pupae, 5.67 % adults). Surveys in the Netherlands from 2003 revealed a number of natural enemies (*H. virescens*, *Parasitylenchus bifurcatus* Poinar & Steenberg (Nematoda: Allantonematidae), *Coccipolipus hippodamiae* and *Dinocampus coccinellae*) attacking *H. axyridis* but only from 2008 onwards (Raak-van den Berg et al. 2014; Table 1). The suggestion is made that after a time lag of 6 years these natural enemies are starting to use *H. axyridis* as a novel host, following host shift from native ladybirds and adaptation to *H. axyridis*.

Recent research has demonstrated that *H. axyridis* individuals contain high numbers of obligate parasitic microsporidia (Vilcinskas et al. 2013). It appears that these microsporidia do not adversely affect *H. axyridis* but cause high mortality when artificially injected into *C. septempunctata* (Vilcinskas et al. 2013). Artificial injection, as used within this study to transmit the microsporidia from *H. axyridis* to *C. septempunctata*, is far removed from the natural mechanisms involved in microsporidia transmission (Solter et al. 2013), so further studies are required to explore the ecological relevance. Indeed further research is needed to understand how the presence of all established alien ladybirds influence parasitism and pathogen infection of declining native ladybirds.

The fungal pathogen *Beauveria bassiana* (Bals.-Criv.) Vuill. (Ascomycota: Cordycipitaceae) commonly infects native species of ladybird (such as *C. septempunctata*), but again, *H. axyridis* seems highly resistant (Roy et al. 2008b). However, in Denmark several entomopathogenic fungi were isolated from overwintering and early season *H. axyridis* (larvae, pupae, adults) including *B. bassiana*, *Isaria farinosa* (Holmsk.) Fr. (Ascomycota: Cordycipitaceae), *Lecanicillium lecanii* (Zimm.) Zare & W. Gams (Ascomycota: Cordycipitaceae), and *L. muscarium* (Petch) Zare & W. Gams (Steenberg and Harding 2009a; Table 1). Similarly, mid-summer surveys in Denmark of all *H. axyridis* life stages revealed infections from the same fungal assemblage with *I.*

farinosa most prevalent, followed by *Lecanicillium* spp. (Howe, Ravn, Jensen, Meyling, unpublished data).

Additional work has assessed the sexually-transmitted ectoparasitic mite *Coccipolipus hippodamiae* (McDaniel & Morrill) (Acari: Podapolipidae) as a biological control candidate against *H. axyridis* (Roy et al. 2011c). This mite, which occurs naturally in Europe and North America (Table 1), causes sterility in female *H. axyridis*, but some native ladybird species are also susceptible to the mite, and thus it does not represent a suitable control strategy for *H. axyridis* (Rhule et al. 2010).

The obligate ectoparasitic fungus *Hesperomyces virescens* Thaxt. (Ascomycota: Laboulbeniaceae) has been capturing the imagination of a number of scientists working on *H. axyridis*. This species has historically received very little attention and so is of particular note. While most Laboulbeniales exhibit a high degree of host specificity, *H. virescens* has been reported from over 30 ladybird species in 15 genera (Bernardi et al. 2014; Ceryngier et al. 2012; Ceryngier and Twardowska 2013; Haelewaters et al. 2016). Transmission of *H. virescens* occurs mainly during sexual contact, as exemplified by the non-random distribution of thalli on the body of males and females (Riddick et al. 2009; Welch et al. 2001); infection can be considered as a sexually transmitted disease (Welch et al. 2001). In *H. axyridis*, however, *H. virescens* is also socially transmitted; in overwintering aggregations, transmission of *H. virescens* through direct physical contact is the most important mechanism of spread (Nalepa and Weir 2007; Riddick 2006). Infection is caused by grooming, resulting in high thallus densities on older hosts (Haelewaters et al. 2012). *Hesperomyces virescens* was reported for the first time on *H. axyridis* in Ohio in summer 2002 (Garcés and Williams 2004). *Harmonia axyridis* is multivoltine, promiscuous, and overwinters in aggregations, all of which contribute to the rapid spread of *H. virescens* and higher infection prevalence on this host, compared to other ladybird hosts (De Kesel 2011). Interestingly, the parasite prevalence of *H. virescens* on *H. axyridis* varies between locations and between years (Haelewaters et al. 2012; Raak-van den Berg et al. 2014). In Belgium, for example, an increase from 0.5 to 96.5 % of parasite prevalence was noted after only 4 years (De Kesel 2011). Currently, *H. virescens* infection of *H. axyridis* is widespread in Western Europe, the eastern

United States and to a lesser extent in South Africa (Haelewaters et al. 2016). *Hesperomyces virescens* has also been reported on *H. axyridis* in its native range with one record from China (Haelewaters et al. 2014). Ongoing work is assessing the influence of (dual) fungal infections on *H. axyridis* and *Olla v-nigrum* (Mulsant), a North American native ladybird species (Haelewaters et al. 2015a).

There is clearly much to uncover about the interactions between *H. axyridis* and natural enemies; global collaborations will provide unique opportunities for exploring these on biogeographic scales.

Conclusions and future directions

Harmonia axyridis has inspired global collaborations and has also been the impetus for understanding biological invasions within and between countries. Many countries have documented the distribution and noted the rapid spread of *H. axyridis* following establishment. Further research is required to improve our understanding of the factors involved in determining the global patterns of invasion by *H. axyridis* which will have wide relevance for invasion biology. Many countries have engaged members of the public in monitoring the distribution of *H. axyridis* and the lessons learnt from such initiatives have been shared and proved informative for developing approaches to citizen science (Gardiner et al. 2012; Pocock et al. 2015; Roy et al. 2012a) and inspiring new projects both within and between countries. Indeed the role of volunteers in monitoring IAS is recognised (Roy et al. 2015b) and there is considerable scope to share resources and technology (August et al. 2015) to increase involvement in monitoring ladybirds and other IAS around the world.

The interactions between *H. axyridis* and other species have fascinated ecologists both in the native and invaded ranges of this species. There has been considerable focus on the potential impacts of *H. axyridis* on biodiversity, particularly intra-guild interactions and specifically IGP. Competitive interactions have received less attention but are worthy of future research emphasis. There is still much to unravel about the interactions between *H. axyridis* and its natural enemies. Comparisons between the native and invaded range will be particularly fruitful. Molecular studies have provided insights into genetic aspects of invasion

and there is certainly more that can be revealed from detailed studies at a global scale. It is exciting to consider the potential of ongoing research to sequence the genome of *H. axyridis* and consider the opportunities that this research might present for future studies (Chown et al. 2015; <http://www.agence-nationale-recherche.fr/?Project=ANR-13-EBID-0001>).

Many of the studies examining the interactions between *H. axyridis* and other species have involved mesocosm experiments under laboratory conditions. There is a need to increase the scale of such studies to consider the negative and positive ecosystem-level impacts of *H. axyridis*. *Harmonia axyridis* contributes to pest control services in a number of crop systems but there is a lack of evidence in relation to ecosystem function and resilience of invaded systems. New molecular methods provide opportunities for detailed studies on the interactions between *H. axyridis* and the diverse range of species with which it interacts. Ecological network analysis represents an appealing and exciting way to explore these complex communities (Roy and Lawson Handley 2012). The coupling of citizen science approaches with global collaborations between researchers will provide the scale of information required to address some of the complex ecological questions that remain unanswered.

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