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- 1 The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and
- 2 ecology
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123 **Abstract**

124 The harlequin ladybird (or multicolored Asian lady beetle), *Harmonia axyridis* (Pallas) (Coleoptera:
125 Coccinellidae), is native to Asia but has been intentionally introduced to many countries as a biological
126 control agent of pest insects. In numerous countries, however, it has been introduced unintentionally.
127 The dramatic spread of *H. axyridis* within many countries has been met with considerable trepidation.
128 It is a generalist top predator, able to thrive in many habitats and across wide climatic conditions. It
129 poses a threat to biodiversity, particularly aphidophagous insects, through competition and predation,
130 and in many countries adverse effects have been reported on other species, particularly coccinellids.
131 However, the patterns are not consistent around the world and seem to be affected by many factors
132 including landscape and climate.

133

134 Research on *H. axyridis* has provided detailed insights into invasion biology from broad patterns and
135 processes to approaches in surveillance and monitoring. An impressive number of studies on this alien
136 species have provided mechanistic evidence alongside models explaining large-scale patterns and
137 processes. The involvement of citizens in monitoring this species in a number of countries around the
138 world is inspiring and has provided data on scales that would be otherwise unachievable.

139

140 *Harmonia axyridis* has successfully been used as a model invasive alien species and has been the
141 inspiration for global collaborations at various scales. There is considerable scope to expand the
142 research and associated collaborations, particularly to increase the breadth of parallel studies
143 conducted in the native and invaded regions. Indeed a qualitative comparison of biological traits
144 across the native and invaded range suggests that there are differences which ultimately could
145 influence the population dynamics of this invader. Here we provide an overview of the invasion history
146 and ecology of *H. axyridis* globally with consideration of future research perspectives. We reflect
147 broadly on the contributions of such research to our understanding of invasion biology while also
148 informing policy and people.

149

150 **Keywords:** Coccinellidae, biocontrol, species traits, competitive interactions, invasion history

151

152 **Introduction**

153 The harlequin ladybird (or multicolored Asian lady beetle), *Harmonia axyridis* (Pallas) (Coleoptera:
154 Coccinellidae), is native to Asia and is a polymorphic, eurytopic species with a broad dietary range
155 (Roy, Brown 2015a). It was widely introduced as a biological control agent of pest aphids, but has
156 spread to many countries within which it was not intentionally released (Brown et al. 2008a). The
157 global invasion of *H. axyridis* has been rapid (Brown et al. 2011b). Concerns about the adverse impact
158 of *H. axyridis* particularly on biodiversity but also to people have motivated research across the world.
159 There have been a number of reviews considering the biology and ecology of *H. axyridis* (Kenis et al.
160 2008; Koch 2003; Koch, Galvan 2008; Majerus et al. 2006; Pell et al. 2008; Pervez, Omkar 2006; Roy,
161 Brown 2015a; Sloggett 2012) often from a regional perspective but this species has an almost global
162 distribution. Therefore, it is timely to provide a world overview of research and perspectives. Indeed,
163 the collaborative nature of the research from around the world on this species is inspiring. As concerns
164 increased with respect to the threats posed by *H. axyridis*, two working groups were established
165 through the International Organisation for Biological and Integrated Control (within the Global and
166 Western Palaearctic Regional Sections) in recognition of the need for collaborative research on the
167 benefits and risks of exotic biological control agents. One of the first outputs from these working
168 groups was the publication of a special issue on *H. axyridis* including 19 manuscripts representing
169 authors around the world (Roy, Wajnberg 2008). *Harmonia axyridis* as both a biological control agent
170 and an invasive alien species (IAS) has informed a range of applied ecological themes, from risk
171 assessment to processes of invasion; *H. axyridis* is considered by many as a model species for
172 understanding processes of invasion (Roy, Wajnberg 2008).

173
174 Here we first consider *H. axyridis* in the context of biological control. We then provide a brief overview
175 of interactions between *H. axyridis* and other species before exploring its current global distribution.
176 We document, on a regional basis, the occurrence and invasion history of *H. axyridis* providing an
177 insight into research priorities and knowledge gaps identified by scientists from around the world.
178 Finally we qualitatively explore the observed traits of *H. axyridis* from both the native and invaded
179 range reflecting on the potential for future collaborations on a global scale.

180

181 ***Harmonia axyridis* and biological control**

182

183 There has been a long history of using ladybirds as biological control agents against various pest insects
184 around the world, beginning with the successful introduction of the vedalia ladybird, *Rodolia cardinalis*
185 (Mulsant) to citrus groves of California (Caltagirone, Douth 1989). *Harmonia axyridis* has a wide diet
186 breadth (reviewed by Hodek and Evans 2012) including many species of aphids, which are the main

187 prey (Osawa 2000) but also other insect taxa (Ohgushi, Sawada 1998). It has been used extensively in
188 classical, augmentative and conservation biological strategies around the world (Koch 2003; Lombaert
189 et al. 2008). There has been considerable research focus on the pest control services provided by *H.*
190 *axyridis* in the native range, particularly in China (Wang et al. 2007a), but also recently in Japan where
191 adults and larvae of flightless *H. axyridis* derived through artificial selection from a Japanese wild
192 population have been used for biological control of aphids mainly in greenhouses (Seko et al. 2014).

193

194 *Harmonia axyridis* was first introduced as a biological control agent in the USA. It is among a number
195 of introduced species of ladybirds that now dominate in many agroecosystems across the USA (Lucas
196 et al. 2007; Obrycki et al. 2009) and *H. axyridis* is considered an important predator of aphid pests in
197 several crops, including pecan (LaRock et al. 2003; Tedders, Schaefer 1994), apple (Brown, Miller
198 1998), citrus (Michaud 2002) and potatoes (Alyokhin, Sewell 2004). In particular, research has focused
199 on the effect of *H. axyridis* on the suppression of the alien soybean aphid, *Aphis glycines* Matsumura
200 (Hemiptera: [Aphididae](#)) (Ragsdale et al. 2011) in soybean, where *H. axyridis* has recently become one
201 of the most abundant coccinellids (Costamagna, Landis 2007; Gardiner, Landis 2007; Gardiner et al.
202 2009a; Gardiner et al. 2009b; Hesler 2014; Liere et al. 2014; Varenhorst, O'Neal 2012). This system,
203 including the overwintering host of *A. glycines*, the European buckthorn *Rhamnus cathartica* L.
204 ([Rhamnaceae](#)) and *H. axyridis*, has been cited as an example of an invasional meltdown, whereby
205 multiple IAS interact synergistically (Heimpel et al. 2010). *Harmonia axyridis* is known to readily
206 consume other predators and parasitoids of aphids (Chacón et al. 2008), but there is a lack of evidence
207 that this impacts on pest control in soybean fields (Costamagna et al. 2008).

208

209 From the mid 1990s, *H. axyridis* was commercialized by a number of biological control suppliers in
210 Western Europe for augmentative biological control of aphid pests in greenhouse crops and urban
211 ecosystems (Coutanceau 2006b; Poutsma et al. 2008). Most commercial suppliers in Europe stopped
212 selling the beetle in late 2003 to mid 2004, with the first reports of nuisance problems and increasing
213 concerns about adverse environmental effects of its establishment. In France, the original strain of *H.*
214 *axyridis* used since 1995 for commercial biological control was replaced in 2000 with a flightless strain
215 developed by INRA (Coutanceau 2006b; Tourniaire et al. 2000). The flightless strain was effectively
216 used to control aphids in hops (Weissenberger et al. 1999). However, the species was never a major
217 player on the European biological control market: at the peak of its commercialisation, it took perhaps
218 5% of the market share of aphidophagous natural enemies (De Clercq, Bale 2011).

219

220 The role of *H. axyridis* in suppressing pest insects in Europe has received less attention than in the USA.
221 In the Czech Republic it has been reported that *H. axyridis* controls pear psylla, *Cacopsylla pyri* (L.)
222 (Hemiptera: Psyllidae), in commercial orchards more effectively than other ladybird species (Nedvěd
223 2014). However, much of the research across Europe has considered the occurrence of *H. axyridis* in
224 crop systems without detailed consideration of effects on aphid populations. In Belgium, the
225 population dynamics of *H. axyridis* in crop systems (wheat, corn, broad bean and potato crops) was
226 studied through field surveys. It has been shown that *H. axyridis* is recorded in such crops 7-8 days
227 after the dominant native ladybirds (Jansen, Hautier 2008; Vandereycken et al. 2013). A one-year
228 study involving field observations in wheat and bean crops in southern England reported an absence
229 of *H. axyridis* in wheat (aphid abundance was reported as low), but presence of *H. axyridis* co-occurring
230 with other ladybirds in bean crops (Wells 2011). *Harmonia axyridis* was the most common aphid
231 enemy species in bean crops and the presence of this species was correlated with high aphid
232 abundance (Wells 2011), perhaps unsurprisingly since the prey biomass required by each single larva
233 to reach the adult stage is very high (Soares et al. 2001, 2003, 2004).

234

235 Even though *H. axyridis* can be considered an effective biological control agent at least from the US
236 studies, the Insurance Hypothesis predicts that control will in the long term be better achieved with a
237 diverse array of natural enemies (Loreau et al. 2003). Since *H. axyridis* tends to depress the diversity
238 of coccinellid assemblages (see below), consistently effective biological control may be threatened by
239 the invasion of *H. axyridis*. Further research is needed to unravel the role of *H. axyridis* as a biological
240 control agent of insect pests. Comparison of aphid populations before and after the arrival of *H.*
241 *axyridis*, or among places with higher and lower abundances of *H. axyridis*, may provide useful
242 information in this respect. Importantly, landscape composition has been found to influence the
243 effectiveness of biological control by *H. axyridis* and other predators. Indeed, soybean fields
244 embedded within diverse landscapes receive a greater pest control service from aphid predators than
245 fields within simplified agricultural landscapes (Gardiner et al. 2009c) compared to landscapes
246 dominated by forests and grasslands where soybean field size was reduced (Woltz, Landis 2014).
247 Similar studies have been carried out in Chile, in regions where *H. axyridis* dominated the
248 aphidophagous communities and again it has been demonstrated that biological control was related
249 to landscape composition with benefits seen through positive associations with the abundance of
250 woodland and urban habitats, but not with fruit crops, in the landscape (Grez et al. 2014a).

251

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

253

254 The wide diet breadth and recognition that *H. axyridis* is a top predator (Pell et al. 2008) has driven
255 predictions that *H. axyridis* has the potential to adversely affect aphidophagous guilds. A number of
256 large-scale analyses have indicated that declines of native ladybirds correlate with the establishment
257 of *H. axyridis*. Indeed declines of native ladybirds have been reported across the USA (Alyokhin, Sewell
258 2004; Bahlai et al. 2014; Colunga-Garcia, Gage 1998; Evans 2004; Harmon et al. 2007; Hesler,
259 Kieckhefer 2008; Losey et al. 2014; Majerus et al. 2006; Wheeler Jr, Hoebeke 1995) and Europe (Roy
260 et al. 2012b). Following the establishment of *H. axyridis* in Michigan a decrease in populations of three
261 species of ladybird has been reported: *Brachiacantha ursina* (F.), *Cycloneda munda* (Say) and
262 *Chilocorus stigma* (Say) (Colunga-Garcia, Gage 1998), followed more recently by a decline in
263 *Coleomegilla maculata* (DeGeer) (Coccinellidae) (Bahlai et al. 2015). However, this last study also
264 noted that declines of several species reported previously from the same site (Colunga-Garcia, Gage
265 1998) appear to have stabilized or reversed, having become statistically undetectable (Bahlai et al.
266 2015). Also in the USA, Michaud (2002) reported *H. axyridis* to be displacing *Cycloneda sanguinea* (L.)
267 in Florida citrus orchards. In the United Kingdom (UK) there is a strong correlation between the
268 declines of seven out of eight native species of ladybird assessed and co-occurrence with *H. axyridis*
269 (Roy et al. 2012b). In Chilean alfalfa fields the abundance of native ladybird species declined after *H.*
270 *axyridis* was first observed in this crop in 2008. Furthermore, total ladybird species and diversity in
271 alfalfa have also declined during this period (Grez & Zaviezo unpublished data). It is thought that the
272 spread of *H. axyridis* has caused the decline of native species, *Adalia bipunctata* (L.) and *Propylea*
273 *quatuordecimpunctata* (L.) in the Ukraine (Verizhnikova 2011) and *C. septempunctata* and *A.*
274 *bipunctata* in Moldova (Iazlovețchii, Sumencova 2013), but this requires confirmation through further
275 research.

276

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

285

286 In Belgium, high niche overlap between *H. axyridis* and generalist native species, particularly *A.*
287 *bipunctata* and *P. quatuordecimpunctata*, was observed, suggesting a high potential for impact of *H.*

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

298

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

307

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

314

315 **Harmonia axyridis and direct competitive interactions**

316

317 The majority of research examining interactions between *H. axyridis* and other aphidophagous species
318 has focused on direct interference competition on other ladybirds, proposing that decline is due to
319 strong asymmetric IGP of eggs and larvae in favour of *H. axyridis* (Pell et al. 2008). This hypothesis is
320 supported by many laboratory and field cage studies around the world (Cottrell 2004; Gardiner, Landis
321 2007; Hoogendoorn, Heimpel 2002; Katsanis et al. 2013; Roy et al. 2008b; Snyder et al. 2004; Soares,

322 Serpa 2007; Ware, Majerus 2008; Ware et al. 2009; Yasuda et al. 2004). Under open field conditions
323 in Ohio, USA, eggs of the exotic *H. axyridis* were subject to lower predation relative to the eggs of
324 native species (Smith, Gardiner 2013). However, out of 342 attacks, video surveillance illustrated that
325 only two were attributable to alien ladybirds (*H. axyridis* feeding on conspecific eggs). Instead, a
326 diverse guild of predators (dominated by Opiliones, Tettigoniidae and the native *C. maculata*) were
327 responsible for the majority of egg attacks (Smith, Gardiner 2013). Importantly, this study accounted
328 only for egg predation but alien and native ladybird species may compete directly through
329 consumption of other life stages. Other tools, such as alkaloid (defensive chemicals within coccinellids)
330 sequestration analyses, frass analysis, and PCR-based gut content analyses, have been developed to
331 quantify the actual extent of interference competition occurring among native and alien species
332 (Brown et al. 2015; Davidson, Evans 2010; Gagnon et al. 2011; Hautier et al. 2008; Hautier et al. 2011;
333 Sloggett et al. 2009; Thomas et al. 2013). For example, Hautier et al. (2011) found that 20.5% of 590
334 *H. axyridis* larvae in Belgium tested positive for native ladybird alkaloids. Thomas et al. (2013) detected
335 the DNA of native ladybirds within *H. axyridis* in the UK, with 3.7-22.7% of 156 *H. axyridis* found to
336 have consumed native species over three years. Gagnon et al. (2011) used molecular gut content
337 analysis to illustrate that IGP among larval ladybirds in soybean fields can be very high; 52.9% of
338 sampled ladybirds contained the DNA of one or more other ladybird species. PCR primers have been
339 developed and used to track aphid and ladybird predation by *H. axyridis* fourth-instar larvae collected
340 in lime trees in Italy, and it was found that 7% of sampled individuals contained the DNA of one of two
341 native ladybird species (Rondoni et al. 2014).

342

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

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

357

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

359

360 *Harmonia axyridis* may also adversely affect aphidophagous species through exploitative competition
361 for shared resources (Evans et al. 2011). Studies to date have failed to show that *H. axyridis* negatively
362 affects native North American ladybirds through exploitative competition among larvae
363 (Hoogendoorn, Heimpel 2004; Yasuda et al. 2004), however, field and microcosm studies reveal
364 reduced fitness in the predatory bug *Anthocoris nemoralis* (F.) (Hemiptera: Anthocoridae) due to
365 competition with *H. axyridis* (Howe et al. 2015)(Howe et al. 2016). Evans (2004) proposed that
366 following the introduction of alien competitors (specifically *C. septempunctata*), native species
367 abandoned croplands due to increased competition for shared prey. Adults of native species were
368 thought to be displaced to ancestral (refuge) habitats not heavily exploited by alien competitors (Evans
369 2004; Snyder 2009). Evans (2004) tested this hypothesis by increasing aphid abundance in a Utah
370 alfalfa fields and found that native ladybirds were drawn back into the field, apparently from refuges
371 maintained in the surrounding landscape. In Japan *Harmonia axyridis* coexists with other predators
372 within natural habitats, without adverse negative impacts on co-occurring species (Osawa 2011).

373

374 ***Alien ladybirds and landscape-scale processes***

375

376 Landscape change can strongly influence species declines within a region (Lindborg, Eriksson 2004).
377 Factors such as habitat degradation, reduction of habitat patch size, and increased isolation of habitats
378 (loss of connectivity) can also lead to declines in the abundance and diversity of coccinellid species
379 within a landscape (Gardiner et al. 2009b; Grez et al. 2013; Grez et al. 2014b). Ladybirds may forage
380 across several habitats within a given landscape including forests, grasslands, and croplands.
381 Landscape changes that alter the distribution of these habitats may affect ladybirds by influencing
382 prey populations, overwintering habitats, or by facilitating the invasion of alien competitors.
383 Observations from several countries suggest that a high proportion of native ladybirds occur in less
384 disturbed habitats, while a high proportion of alien ladybirds (including *H. axyridis*) occurs in human-
385 modified habitats (Grez et al. 2013; Panigaj et al. 2014).

386

387 Landscape composition and heterogeneity can also affect competitive interactions among coccinellids
388 (Gardiner et al. 2009a; Gardiner et al. 2009b). In the USA, alien species were more abundant within

389 soybean fields embedded within forested landscapes, and native species more common in agricultural
390 landscapes with significant forage and grassland habitat. A large-scale study assessing the influence
391 of landscape factors on the spread of *H. axyridis* across the UK indicated that coniferous woodland
392 may negatively affect the spread of this species (Purse et al. 2014). Further research is needed to
393 examine how the composition of the surrounding landscape influences the stability of native
394 populations in the invaded regions.

395

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

397

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

412

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

422

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

438

439 A push-pull strategy including artificial injury of selected fruit clusters on the vineyard margin and
440 spraying the adjacent rows with bisulphite has been proposed as a management option (Glemser et
441 al. 2012; Nedvěd 2014). In addition, progress has been made in developing both natural and synthetic
442 corks that can significantly reduce MP concentrations in wine (Pickering et al. 2010). However, more
443 research is needed to evaluate this approach for additional varietal sources and cost effectiveness.
444 The establishment of *H. axyridis* in regions where the production of wine is economically important,
445 including Crimea, the Caucasus, Canada, Europe, South Africa and South America, continues to be a
446 concern, and close monitoring of the populations in these countries is critical.

447

448

449 **Global distribution and regional research priorities**

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

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

459

460 **Asia**

461 *Harmonia axyridis* is native to East Asia (Mongolia, parts of China and Russia, northern Vietnam, Japan
462 and Korea) (Figure 1).

463

464 *China*

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

472

473 *Japan*

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

479

480 *Asian part of Russia, Kazakhstan and Kyrgyzstan*

481

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

489

490 The native range of *H. axyridis* includes in the Altai Mountains, situated in north-eastern Kazakhstan
491 and West Siberia. In some recent studies, the south-east of Kazakhstan was regarded as part of the
492 native range (Loiseau et al. 2009; Lombaert et al. 2014; Lombaert et al. 2011). However, this is
493 incorrect because *H. axyridis* was not recorded in the south-east of Kazakhstan in the nineteenth
494 century or in the first half of the twentieth century. In 1968–1970 attempts to introduce *H. axyridis*
495 from the Far East to the south-east of Kazakhstan for biological control of aphids (Savojskaja 1971)
496 failed. Now *H. axyridis* is a common species in the south-east of Kazakhstan and was recently detected
497 in the neighbouring region of Kyrgyzstan. Both morphological and genetic studies strongly indicate
498 that the *H. axyridis* occurring in this region are not descendants of the released beetles, since current
499 populations are similar to West-Siberian populations and differ from Far East populations. It is
500 hypothesised that *H. axyridis* appeared in south-eastern Kazakhstan and Kyrgyzstan after the
501 construction of the Turkestan-Siberian Railway, and that the beetles spread along this railway (Orlova-
502 Bienkowskaja et al. 2015).

503

504 *European part of Russia, Moldova, Ukraine and Belarus*

505 Releases of *H. axyridis* for biological control of aphids in the Soviet Union began about 80 years ago.
506 Attempts to introduce *H. axyridis* were made in Transcaucasia in the 1930s, in the Chernovtsy region
507 (Ukraine) in 1964, in the Kiev region (Ukraine) in the 1960s, in Crimea in 1969, in the Tashkent region
508 (Uzbekistan) in 1969, in Minsk (Belarus) in 1968-1970, in south-eastern Kazakhstan in 1968–1970 and
509 in Adjara and Mtsheta region (Georgia) in 1982-1988. It is thought that none of the intentionally
510 released populations established (Izhevsky 1990; Verizhnikova, Shylova 2013a). Established
511 populations are thought to have originated from secondary spread eastward of *H. axyridis* from
512 western Europe to European Russia and neighbouring countries. Established populations were
513 detected in the Kaliningrad region (Russian enclave in the Baltic region) (Zakharov et al. 2011).
514 Recently, *H. axyridis* has been observed spreading rapidly in the Caucasus and the south of European
515 Russia (Orlova-Bienkowskaja 2014). Established populations have been found in Adygea, Krasnodar
516 region, Abkhazia, the Stavropol region, Georgia (Belyakova, Reznik 2013), Crimea (Rybalchenko,
517 personal communication), Daghestan (Ilyina, personal communication) and Rostov region (Arzanov,
518 personal communication). Individual specimens of *H. axyridis* have also been found in the central belt
519 of European Russia (Belgorod and Lipetsk regions) (Orlova-Bienkowskaja 2013; Ukrainsky, Orlova-
520 Bienkowskaja 2014), but it is unknown if the species is established there.

521

522 In 2003, several specimens of *H. axyridis* f. *spectabilis* were found in the wild in Kiev (Ukraine) and
523 since 2007 a stable population of *H. axyridis* has existed there (Verizhnikova, Shylova 2013b). In 2009

524 *H. axyridis* was detected in several locations in western Ukraine, and there has been rapid expansion
525 since, with the species now abundant all over the country (Nekrasova, Tytar 2014). The spread of *H.*
526 *axyridis* has been so rapid that it has been observed to occur across a whole country before being
527 detected: *H. axyridis* was not detected in Moldova until 2011, when it had already become common
528 throughout the country (Timuş, Stahi 2013).

529

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

533

534 Current research in Russia and the Ukraine relates to the development and effects of photoperiod on
535 development and maturation (Belyakova, Reznik 2013; Reznik et al. 2015), genetics (Zakharov et al.
536 2011), morphological variability (Blekhman 2008), population dynamics (Nekrasova, Tytar 2014) and
537 current expansion of the range in Russia and adjacent countries (Ukrainsky, Orlova-Bienkowskaja
538 2014). There is also considerable interest in elucidating the routes of invasion by genetic methods as
539 has been done for many other regions (Lombaert et al. 2014). It is possible that the populations in the
540 Caucasus and in the south of European Russia include hybrids between invasive European individuals
541 and those introduced from the Far East for use in biological control. As the secondary range is
542 expanding eastwards, it is predicted that it will soon reach the western border of the native range.
543 Thus there is an opportunity to observe the consequences of interactions between native and invasive
544 populations in West Siberia.

545

546 **North America**

547 *Hamonia axyridis* was repeatedly introduced throughout the twentieth century to the USA with the
548 aim of establishing sustaining populations (Gordon 1985; Harmon et al. 2007; Koch et al. 2006b).
549 Intentional releases of *H. axyridis* include a number of states but notably California in 1916, and
550 multiple eastern states from 1978 to 1992 (Chapin, Brou 1991; Gordon 1985; McClure 1987; Tedders,
551 Schaefer 1994). *Harmonia axyridis* was first detected beyond intentional release sites in the United
552 States in 1988 in south-eastern Louisiana and eastern Mississippi (Chapin, Brou 1991). A second,
553 independent set of releases led to establishment in the 1980s in the Pacific Northwest (LaMana, Miller
554 1996; Lombaert et al. 2014; Lombaert et al. 2010). It is unknown whether all established populations
555 resulted from these releases or from additional, accidental introductions. Nonetheless by the mid-
556 1990s, *H. axyridis* had been found across the country with detection reports from 45 of the 48
557 contiguous states by 2007 (Dreistadt et al. 1995; Hesler et al. 2001; Krafur et al. 1997; LaMana, Miller

558 1996; Mizell III 2007) and most recently from Montana in 2009 (Foley et al. 2009) and Arizona in 2008
559 (Fothergill et al. 2010). *Harmonia axyridis* was first detected in Canada in 1994 (Coderre et al. 1995).
560 Currently this species is found throughout most of North America north of Mexico with Labrador,
561 Saskatchewan, Alaska and Wyoming the only areas where it has not yet been reported (Foley et al.
562 2009; Fothergill et al. 2010; Hicks et al. 2010; Koch et al. 2006b). *Harmonia axyridis* is also established
563 and widespread in Mexico (Brown et al. 2011b).

564

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

572

573 **South America**

574 *Harmonia axyridis* is reported in most countries in South America (Amat-García et al. 2011; González,
575 Kondo 2012; Koch et al. 2011; Kondo, González 2013; Nedvěd, Krejčík 2010; Saini 2004; Solano, Arcaya
576 2014). Based on factors such as climate and habitat, it has been predicted that *H. axyridis* would
577 become established across broad areas of South America (Koch et al. 2006b). The invasion by *H.*
578 *axyridis* has been followed intensively in Chile.

579

580 *Chile*

581 In 1998, a flightless strain of *H. axyridis* was introduced from France to central Chile for biological
582 control in greenhouses, but those populations did not establish (Grez et al. 2010) (Table 1). In 2003,
583 large numbers of flying *H. axyridis* associated with aphids in poplar trees were reported near the
584 release sites. In 2008, surveys of ladybird populations in alfalfa revealed only one individual *H. axyridis*
585 (from a sample of approximately 90,000 ladybirds), but rapid population increase was observed over
586 the next two years in alfalfa and other habitat or crop types (Grez et al. 2010). *Harmonia axyridis* is
587 currently one of the two most abundant species in alfalfa fields in central Chile, representing 50 - 90%
588 of ladybirds (Grez et al. 2014a; Grez et al. 2014b). It is expanding into other habitats, including native
589 vegetation, such as sclerophyllous matorral, although at very low densities (Grez et al. 2013).
590 *Harmonia axyridis* is spreading toward southern Chile, colonizing regions with colder climates. In
591 contrast, few records are reported towards northern Chile, where the Atacama Desert is probably

592 acting as a barrier for its invasion. From its original distribution in 2010, covering a range of 250 km
593 (north to south) near Santiago, it has expanded its distribution to ~2600 km (north to south), and from
594 sea level to >3000 m a.s.l., with a north to south spread of approximately 160 km year⁻¹. Genetic
595 analyses suggest that current Chilean populations come from the East North America strain (Lombaert
596 et al. 2014), representing an accidental introduction. Only *f. succinea* has been found in Chile.

597

598 Current research in Chile relates to the impacts of this species on the diversity of ladybird assemblages
599 and abundance, including native species, in different habitats, as well as its potential damage to
600 vineyards. There are also extensive field and laboratory experiments in progress to assess IGP and
601 competition as mechanisms for understanding the dominance of *H. axyridis* over other ladybirds.
602 Studies of physiological performance and life history traits under different temperature conditions in
603 the laboratory have also been carried out (Barahona et al. submitted). The invasion process is being
604 systematically tracked through surveys coordinated by Grez and Zaviezo, including data from the
605 Surveillance Department of the National Agrarian and Livestock Service (SAG), and from media and
606 social networks specifically developed for this purpose (web page: www.chinita-arlequin.com;
607 Facebook: <https://www.facebook.com/chinita.arlequin>; twitter:
608 <https://twitter.com/chinitaarlequin>). The high interest and participation of citizens through these
609 media suggest that the presence of *H. axyridis* is of growing concern to Chileans.

610

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

621

622 The main gaps in knowledge in Chile relate to natural enemies and possible control or containing
623 methods. The only observed natural enemy thus far is the parasitoid *D. coccinellae*. Also, there are
624 many unanswered questions in relation to the ecology and biology of *H. axyridis* during summer time,
625 when this species disappears from crops, apparently estivating or migrating to other, as yet

626 undetermined, locations. Its role as a biological control agent of aphids and other pests is still
627 unknown.

628

629 **Europe**

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

637

638 *Austria*

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

645

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

651

652 *Belgium*

653 In Belgium, *H. axyridis* was first applied as a biological control agent in 1997. The species was first
654 observed in the wild in 2001 (Adriaens et al. 2003) and this led to the end of its commercial use in
655 Belgium. In less than five years the species invaded the entire country, its distribution covering all
656 Belgian ecoregions (Adriaens et al. 2008). The area of occupancy showed an average rate of increase
657 of 189% (5000 km²) per year from 10.000 km² in 2002 to 31.000 km² in 2006. *Harmonia axyridis* has
658 become the most abundant species in (semi-)natural systems and also dominates the aphidophagous
659 guilds in certain agro-ecosystems (Vandereycken et al. 2013).

660

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

667

668 *Czech Republic*

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

677

678 *Denmark*

679 *Harmonia axyridis* was first recorded in Copenhagen 2006, and presumed to have arrived from
680 Germany (Brown et al. 2008a; Pedersen et al. 2008). In the following years the beetle spread within
681 the Greater Copenhagen area, becoming established across the island of Zealand. By 2007/8, its
682 spread continued westwards to the islands of Lolland, Langeland, Ærø, and in the east to Bornholm
683 (perhaps arriving from Poland or Germany) where populations are now established (Howe 2015; Howe
684 et al. 2015; Steenberg, Harding 2009b; Steenberg et al. 2009). By 2008, *H. axyridis* had reached Jutland
685 in the far west of Denmark (Steenberg et al. 2009). The most northern record to date (latitude 57° N)
686 was from produce in a supermarket, highlighting the potential for spread through anthropogenic
687 pathways. Data from Zealand indicates stable populations with *H. axyridis* dominating ladybird
688 assemblages where established. Greatest densities occur within urban areas of central Copenhagen
689 (Ravn and Howe, unpublished data).

690

691 It is interesting to note that the distribution of *H. axyridis* in Denmark is limited in the north of the
692 country. Indeed, following ten years' of establishment within Denmark, aside from the
693 aforementioned supermarket record there are no records of *H. axyridis* north of 56 ° N (Ravn and

694 Howe, unpublished date), which corresponds with a lack of records from Scotland (UK). Whether this
695 represents a true limit to the northern distribution attributable to present climatic conditions requires
696 further research, particularly in relation to future predictions of spread based on expected climate
697 warming.

698

699 *France*

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

715

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

726

727 Using population genetic approaches, it has been shown that the *H. axyridis* sampled across France

728 (see below for exceptions) belonged to a single genetic unit that has invaded the Western part of
729 Europe (Lombaert et al. 2010; Lombaert et al. 2011). This invasive population bears traces of genetic
730 admixture between an eastern North American wild source, which was found to have served as a
731 “bridgehead source” for many worldwide invasive outbreaks, and a biological control strain used in
732 Europe (Lombaert et al. 2010). Experimental studies in the laboratory have investigated the
733 phenotypic impacts of such genetic admixture (Facon et al. 2011; Tayeh et al. 2013; Tayeh et al. 2012;
734 Tayeh et al. 2015; Turgeon et al. 2011). Biological control individuals were found to display classic *r*-
735 selected traits with a shorter lifespan and an earlier egg production when compared to native and US
736 invasive individuals. European invasive individuals have shown phenotypic traces of the genetic
737 admixture between US invasive and biological control individuals. For most traits (such as age at the
738 start of reproduction, total adult and reproductive lifespan), European invasive individuals displayed
739 intermediate values between both parents. Thus genetic admixture has had a long-lasting effect in the
740 wild by shaping the life-history strategy of the European invasive individuals of *H. axyridis*. In France,
741 and more generally Western Europe, the exact role of admixture with the European biological control
742 strain in the process of invasion remains poorly known. The single eastern North American origin of
743 one South African and two South American outbreaks indicates that the genetic admixture observed
744 in Western Europe is not required for an eastern North American propagule to establish and start an
745 invasive population in diverse ecological contexts (Lombaert et al. 2014). It seems therefore unlikely
746 that admixture in Western Europe has radically changed the outcome from failed to successful
747 invasion. Such admixture has probably simply modulated the rate (or impact) of an invasion process
748 that would have been successful anyway.

749

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

759

760 *Germany*

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

769
770 Several German populations from 2008 and 2009 were examined for the presence of antagonistic
771 microorganisms (bacteria, fungi, microsporidia) and invertebrate parasites (Herz, Kleespiel 2012).

772

773 *Italy*

774 In Italy, *H. axyridis* was released in protected crops as a biological control agent from 1995 to 1999.
775 However, the use of *H. axyridis* for biological control was suspended because concerns over adverse
776 impacts became apparent. The first occurrence of establishment was in 2006 in Piedmont followed by
777 subsequent observations in Emilia-Romagna in 2008 and rapid establishment in 16 out of 20 Italian
778 regions with particularly widespread occurrences across northern and central Italy (Burgio et al.
779 2008b; Cornacchia, Nardi 2012). The origin of the populations is unknown; individuals could be either
780 offspring of those released *in situ* or immigrants from other parts of Italy, France or Switzerland
781 (Burgio et al. 2008b).

782

783 Research studies in Italy have focused on *H. axyridis* biology (Bazzocchi et al. 2004) and specifically life
784 table parameters. Research on the occurrence of parasitoids attacking *H. axyridis* is ongoing (Francati
785 2015a, b; Rondoni et al. 2013a; Rondoni et al. 2013b). Other studies are focusing on the development
786 of a liver-based artificial diet, which could assist in maintenance of cultures of adult *H. axyridis*
787 (Sighinolfi et al. 2008), and on the susceptibility of *H. axyridis* larvae to lambda-cyhalothrin insecticide
788 (Benelli et al. 2015).

789

790 *Norway*

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

795

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

800

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

812

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

822

823 *Slovakia*

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

829 gardens, orchards and urban areas. The records from 2008–2012 document the invasion clearly
830 (Panigaj et al. 2014). The distribution and time sequence of the records support the maximum rate of
831 the spread of *H. axyridis* to be approximately 200 km year⁻¹, the spread being accelerated by human
832 movement (Panigaj et al. 2014). The local topography played a crucial role in the spread: 47% of the
833 records of the coccinellid were from lowlands (94–200 m), 36% from low hilly areas (200-400 m), 11%
834 from moderate altitudes (400-600 m) and only 6% from higher areas (600-1250 m a.s.l.) (Panigaj et al.
835 2014). Despite great efforts in 2013 and 2014, only a single specimen of *H. axyridis* was recorded from
836 altitudes above 1000 m.

837

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

844

845 *Switzerland*

846 The first *H. axyridis* adult was found in 2004 in Basel (Klausnitzer 2002), but it was only in 2006 that
847 establishment was confirmed in several locations (Eschen et al. 2007). From then, the ladybird rapidly
848 invaded all areas of low and middle altitudes within two years. A long-term inventory was initiated in
849 the northwest of Switzerland in 2006 to record the impact of *H. axyridis* on native ladybirds (Eschen
850 et al. 2007). Ladybird populations were monitored using standardised sampling methods at 45 sites:
851 15 broadleaved hedgerows, 15 meadows and 15 conifer sites several times a year. The monitoring
852 was interrupted only in 2014 but has since restarted. Other surveys were made in other habitats on
853 an irregular basis, in particular on urban trees. Since 2008, *H. axyridis* has become by far the most
854 abundant ladybird on broad-leaved shrubs and trees, accounting for 60 to 80% of all ladybirds
855 collected throughout the year. In contrast, in meadows and on conifers, *H. axyridis* still remains rather
856 uncommon, except on some specific plants such as nettle (Kenis and Eschen, unpublished data).

857

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

863

864 *The Netherlands*

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

875

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

886

887 Research in the Netherlands has focused on natural enemies (Haelewaters et al. 2012; Raak-van den
888 Berg et al. 2014; Sloggett 2010) and the high overwintering survival of *H. axyridis* (70.8-88.2%) (Raak-
889 van den Berg et al. 2012). The latter study found that overwintering survival was higher (1) at sheltered
890 places compared to exposed sites and (2) when ladybirds were overwintering at south-western sides
891 of buildings. As a comparison, winter survival of *A. bipunctata* in the Netherlands is 17-78% (Brakefield
892 1985).

893

894 *United Kingdom*

895 The UK has a long history of involvement of volunteers in gathering information on wildlife through
896 biological recording (Pocock et al. 2015; Roy et al. 2015a). The Coccinellidae Recording Scheme

897 (hosted by the Biological Records Centre which is part of the Centre for Ecology & Hydrology) was
898 established in 1971 (Roy et al. 2011a). The legacy of ladybird recording in the UK provided a unique
899 dataset through which to explore the impacts of *H. axyridis* on other ladybirds. *Harmonia axyridis*
900 arrived in Britain through dispersal and introduction events from regions (mainly Europe) in which it
901 was deliberately released as a biological control agent (Brown et al. 2008b). *Harmonia axyridis* was
902 first recorded in the UK in 2003 (Roy et al. 2012d) and was established by 2005. An on-line survey
903 (www.ladybird-survey.org) was launched to monitor the spread of *H. axyridis* while promoting the
904 continued recording of other ladybirds. Tens of thousands of people have provided records of *H.*
905 *axyridis* and other species of ladybirds (Roy et al. 2015b), providing an invaluable large-scale and long-
906 term dataset which has been used to explore the invasion process and concomitantly trends in the
907 distribution of other ladybirds (Comont et al. 2014a; Comont et al. 2012; Purse et al. 2014; Roy et al.
908 2012c). For example, declines in the distribution of seven (of eight assessed) native species of ladybird
909 have been demonstrated, and correlated with the arrival of *H. axyridis*, using the records collated
910 through the UK Ladybird Survey (Roy et al. 2012c).

911

912 The rapid spread of *H. axyridis* - more than 100 km per year across the UK (Brown et al. 2008b) - has
913 been attributed to its high natural dispersal capability through both flight (Jeffries et al. 2013;
914 Lombaert et al. 2014; Maes et al. 2014) and anthropogenic transport (Brown et al. 2011b). A number
915 of factors are considered to have contributed to the successful establishment and dominance of this
916 polymorphic species within aphidophagous guilds across the UK, including high reproductive capacity,
917 intra-guild predation, eurytopic nature and high resistance to natural enemies within the invaded
918 range (Roy, Brown 2015b).

919

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

926

927 **Africa**

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

931

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

941

942 Unaware of the above, (Stals, Prinsloo 2007) announced that *H. axyridis* was first recorded in South
943 Africa in 2004, in the Western Cape Province. However, museum records later revealed that adults
944 and immature stages had been found in the Cape Town area as early as 2001 (Stals 2010). This remains
945 the earliest known date and location of establishment in southern Africa. Sabie, the 1980s release
946 point, is c. 1,800 km away from Cape Town. *Harmonia axyridis* specimens from the Sabie area were
947 only recorded in the austral summer of 2008 (Stals unpublished), when the contemporary spread of
948 the invader into Mpumalanga was already well underway (Stals 2010).

949

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

954

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

962

963 *Harmonia axyridis* rapidly spread widely through much of South Africa (Stals 2010; unpublished). It
964 seems established largely in cooler and more mesic parts of the country, viz. the south-western,

965 southern and interior-eastern Cape regions, and the more northern eastern and east-central areas,
966 with few records from the semi-arid western and west-central reaches or the hot northern regions.
967 No records have as yet come from the subtropical eastern coastal belt. The invader is well established
968 and commonly encountered in the Fynbos and Grassland Biomes; established and not infrequently
969 encountered in the Savanna Biome; but infrequently reported from other biomes. In South Africa, the
970 majority of records come from urban and rural gardens or dwellings, and from agricultural land. Other
971 southern African countries with records of *H. axyridis* are Lesotho (first record June 2008, Stals 2010)
972 and Swaziland (first record November 2013, Stals unpublished), and the ladybird has likely established
973 in both these countries.

974

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

982

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

992

993 However, many research aspects that are key for evaluating the establishment, spread and impact of
994 *H. axyridis* are lacking. No systematic field surveys are taking place and therefore the invader's
995 abundance across habitat types is also unknown. More importantly, data on the native ladybird
996 communities (species richness and abundance) occurring in areas with and without *H. axyridis* are not
997 being collected and the impacts on these communities are thus unknown. Of overriding importance
998 may be the complete lack of baseline data prior to this invasion; it is possible that no readily

999 comparable and uninvaded habitats may remain for urgent collection of baseline information. In
1000 addition, the taxonomy and phylogeny of the native Coccinellini need to be examined, in particular
1001 those African species currently placed in the genus *Harmonia*.

1002

1003 Under South African national legislation, *H. axyridis* is a Category 1b Listed Invasive Species
1004 (Department of Environmental Affairs South Africa 2014a), which in terms of the National
1005 Environmental Management: Biodiversity Act, 2004, legally is a “species which must be controlled”
1006 (Department of Environmental Affairs South Africa 2014b). How such control is to be achieved is
1007 unclear at present.

1008

1009 ***Failure of Harmonia axyridis to establish in some regions***

1010 *Harmonia axyridis* is much more commonly and widely distributed in the northern than in the
1011 southern hemisphere, perhaps unsurprising given its Asian origin. While *H. axyridis* distribution
1012 extends to boreal regions in its native range, its invasive distribution in the north and south of Europe,
1013 and also in northern Canada and Alaska, is more limited and suggests that climatic factors may be
1014 important in limiting the spread of this species. Globally, there are very few records from tropical
1015 regions (23.4°N–23.4°S); where it has been reported from the tropics it is not widely spread (e.g.,
1016 Colombia, Venezuela, Kenya, Tanzania). In both South America and Africa, limits to its distribution
1017 apparently include warm tropical but also arid environments.

1018

1019 In Europe there are some habitats and regions that appear to be resistant to the establishment of *H.*
1020 *axyridis*. Some examples are the limited evidence of establishment in Greece (Kontodimas et al. 2008),
1021 Turkey (Bukejs, Telnov 2015), Spain, including the Canary Islands (Goldarazena, Calvo 2007; Jacas et
1022 al. 2006; Pons et al. 2015), Bosnia and Herzegovina (Kulijer 2010), Portugal, including the Madeira and
1023 Azores archipelagos (Garcia 1986; Soares et al. 2008), Northern Ireland (Murchie et al. 2008), the
1024 Republic of Ireland (<http://www.invasivespeciesireland.com>), and Réunion (Quilici, pers. com). It is as
1025 important to consider the regions in which *H. axyridis* has failed to establish as those in which it has
1026 succeeded. Only recently has consideration been given to understanding invasion failures within the
1027 context of invasion processes (Zenni, Nuñez 2013). The factors limiting invasion by *H. axyridis* in some
1028 geographic areas are worthy of exploration and could potentially provide insights into whether the
1029 southern and northern European ecosystems are more resilient to invasion than other parts of Europe
1030 and beyond. Investigation of equivalent patterns on the southern African subcontinent would also be
1031 informative.

1032

1033 Records of successful breeding by *H. axyridis* are very limited in Scotland (Roy, Brown 2015b) and
1034 although climatic conditions are not thought to have been a barrier to the colonization and spread of
1035 *H. axyridis* in southern Britain, it is possible that climate has limited its abundance not only in northern
1036 England and Scotland (Brown et al. 2008b; Roy, Brown 2015b), but also Denmark (Steenberg, Harding
1037 2009b) and further north throughout Scandinavia. The combination of lower temperatures and higher
1038 precipitation in Scotland compared to England could be limiting the distribution of *H. axyridis* within
1039 Scotland. The Orkney and Shetland Islands are considered climatically unsuitable for *H. axyridis*
1040 (Poutsma et al. 2008), and in support of this there have only been occasional records of adults, arriving
1041 on produce imported from the mainland, from these northern islands (Ribbands et al. 2009). There
1042 are no records of immature stages of *H. axyridis*, or other ladybird species, on these islands.

1043

1044 Although thousands of individuals of both f. *succinea* and f. *conspicua* have been released in the
1045 Azores (Garcia 1986; Schanderl et al. 1992), *H. axyridis* has not become established there (Evans et al.
1046 2011; Soares et al. 2008). It has been hypothesised that prey features related to local plant habitats
1047 and landscape structure, together with the ladybird characteristics in terms of body size, might explain
1048 why the invader is absent (Hemptinne et al. 2012). The coastal terrestrial habitats that form 9% of the
1049 landscape are the richest in terms of food resources for aphidophagous ladybirds. It is predicted that
1050 other large and medium-sized species of ladybirds (*Coccinella undecimpunctata* L.), which have
1051 requirement for high prey consumption, will also decline because of shortage of prey (Borges et al.
1052 2006; Cabral et al. 2006; Sebastião et al. 2015; Soares et al. 2001) for example *C. septempunctata* is
1053 considered extinct from the Azores. The Azorean communities are nowadays dominated by minute
1054 Scymnini species and larger species are no longer recorded. Despite the competitive advantage of *H.*
1055 *axyridis* against the native *C. undecimpunctata* (Felix, Soares 2004; Nória et al. 2008), it is apparent that
1056 Azorean habitat characteristics and the high feeding rate of *H. axyridis* are hampering its invasion.

1057

1058 **Comparison of traits**

1059 There have been a number of studies examining the influence of life-history traits on invasion and *H.*
1060 *axyridis* is no exception (Comont et al. 2014a; Comont et al. 2012). The traits databases compiled for
1061 these studies provides a rare opportunity to explore variation in life-history traits between localities
1062 (native and invaded) around the world. Extending and combining traits databases to a global scale will
1063 provide intriguing insights. The invasion process and ecological attributes (Table 1) and the
1064 compilation of life history traits of *H. axyridis* (Table 2) represents the start of this process and
1065 highlights gaps in understanding. However, qualitative comparisons of the traits of *H. axyridis* across
1066 the invaded range and with the native range reveals patterns that are worthy of further investigation.

1067

1068 *Habitat*

1069 The habitat of *H. axyridis* is wide and although poorly documented in many regions the exploitative
1070 and opportunistic nature of this species is evident (Table 1). During early stages of invasion it has been
1071 noted that *H. axyridis* is more prevalent within urban and agricultural landscapes than in semi-natural
1072 landscapes (Brown et al. 2008b; Grez et al. 2014a; Grez et al. 2014b). *Harmonia axyridis* is common
1073 within gardens and parks throughout the year and its presence in agricultural fields, orchards or
1074 vineyards has been documented globally and local damage due to quality loss of fruits is known (Koch
1075 et al. 2004a). Across Europe and Japan *H. axyridis* is commonly associated with trees and shrubs. For
1076 example in urban areas in Europe it is the most abundant ladybird on lime (*Tilia* spp.) and maple trees
1077 (*Acer* spp.) but is also frequently found on Scots pine, *Pinus sylvestris* L. (Pinaceae). The habitats of *H.*
1078 *axyridis* in Japan are disturbed areas such as agricultural fields, orchards, parks, residential yards and
1079 gardens (Osawa 2011) and *H. axyridis* is generally uncommon in natural forests (Osawa 2011).

1080

1081 In winter *H. axyridis* has a propensity to aggregate in buildings. Across Europe adults usually start
1082 aggregating in October and leave overwintering sites in April. The aggregating behaviour has been
1083 shown to depend on two blends of long chain hydrocarbon molecules, one leading conspecifics
1084 towards aggregation sites and the other ensuring cohesion of the aggregations (Durieux et al. 2012).
1085 These findings, with the identification of a volatile sex pheromone in female *H. axyridis* (Verheggen et
1086 al. 2007), might offer some potential in the development of specific control methods for *H. axyridis*.

1087

1088 It is critical that we have a better understanding of the habitat preference and suitability of *H. axyridis*;
1089 this is especially relevant when facing current global environmental change, especially urbanization,
1090 agricultural intensification and climate change which will undoubtedly affect the spread and
1091 distribution of *H. axyridis*. Habitat suitability could be estimated using Species Distribution Models
1092 based on fine-scale records on the presence/absence or densities of *H. axyridis* populations. Such
1093 results would have wide relevance to invasion biology.

1094

1095 *Diet breadth*

1096 The wide diet breadth of *H. axyridis* is evident from Table 1 and, as already stated, includes pest and
1097 non-pest insects but also fruits. Perhaps of most interest, and relevance to understanding the threat
1098 posed by this species to biodiversity, is the range of non-pest insects consumed and associated
1099 population-level effects. Much research has focussed on interactions between *H. axyridis* and other
1100 coccinellids (Pell et al. 2008) but there is a need for further work on other taxonomic groups for

1101 example expanding the research on butterflies such as the studies on the monarch butterfly *Danaus*
1102 *plexippus* (L.) (Koch et al. 2006a; Koch et al. 2003). Furthermore it is critical that future research
1103 considers the population-level effects of *H. axyridis* on different species and implications for
1104 ecosystem function. Current studies have not clearly documented the diet preference, adaptability
1105 and feeding efficiency of *H. axyridis*, which are essential for assessing its potential impact in recipient
1106 ecosystems.

1107

1108 *Thermal tolerance*

1109 Only a few studies, representing populations of *H. axyridis* from a few regions, have considered
1110 thermal tolerance (Table 2) (Koch et al. 2004b). Of particular importance would be to measure lower
1111 and upper temperature tolerance of several life stages using ecologically relevant conditions for the
1112 population examined. Indeed to build Species Distribution Models, thermal tolerance needs to be
1113 carefully measured in the laboratory so that the reaction norm of physiological/behavioural
1114 performance as a function of ambient temperature can be established. However, *H. axyridis* usually
1115 overwinters in shelters and aggregations and cold tolerance measurements should be interpreted in
1116 regards to ecologically relevant conditions. Indeed *H. axyridis* can be found at a range of altitudes: in
1117 Chile individuals have been found at >3000 m a.s.l. while in central Europe it is regularly present from
1118 the eastern lowlands (114 m a.s.l.) to montane/subalpine forests (approx. 1600 m a.s.l., unpubl. data)
1119 in the Alps, with one isolated record of a probable wind-drifted individual at 2280 m a.s.l. in Carinthia.

1120

1121 Although laboratory studies show that invasive populations of *H. axyridis* do not survive at 34°C
1122 (Benelli et al. 2015), the species has been documented in Kenya (Nedvěd et al. 2011) and Tanzania
1123 (Nedvěd, Háva 2015) but there is no evidence that this species is abundant in the tropics. In addition,
1124 the wide spread and occurrence of *H. axyridis* in mesic cool climates or pockets of urban gardens
1125 within drier environments in its novel range suggests that climatic factors other than temperature may
1126 also play a role in shaping its distribution.

1127

1128 Desiccation resistance (Nedved, Kalushkov 2011) and the potential cross-effects of temperature and
1129 humidity on temperature limits may provide useful information for modelling its future distribution in
1130 face of climate change (Hoffmann et al. 2013). Perhaps more importantly, the study of the plasticity
1131 and evolutionary adaptation of tolerance limits in *H. axyridis* using both native and invasive
1132 populations would provide insights into its adaptive capacity to future climatic challenges. The effect
1133 of different climate regimes on the body weight and fat body content of *H. axyridis* and *C.*
1134 *septempunctata* has been the focus of laboratory studies in Germany (Krengel et al. 2012). This study

1135 concluded that that *C. septempunctata* has life history adaptations that would confer an advantage
1136 over *H. axyridis* at elevated temperatures.

1137

1138 *Reproductive potential*

1139 A number of traits (voltinism, fecundity and egg hatching success) reveal the high reproductive
1140 potential of *H. axyridis* (Table 2). In the native range, *H. axyridis* is generally considered to have two
1141 generations per year, although it can have three and occasionally up to eight generations in some
1142 years and localities (Osawa 2011). In Kyoto, in the centre of Japan, the overwintering adults mate and
1143 lay eggs in spring (Osawa 2000). The adults of the first generation emerge in mid May to June (Osawa
1144 2000). In mid summer, the beetles aestivate in small groups in leaf-shelters on trees and the behaviour
1145 is regarded to be an adaptation to high temperature (Toda, Sakuratani 2006). In autumn, *H. axyridis*
1146 adults fly towards overwintering sites, white or pale objects on hilltops or valleys, where they
1147 aggregate from early November (Obata 1986).

1148

1149 Within much of the invaded range, *H. axyridis* only achieves two generations per year, whereas in the
1150 native range up to eight generations have been observed. Increases in global temperatures could
1151 facilitate an increase in voltinism, and corresponding increase in abundance across the invaded range
1152 in the future. On the contrary, increase in temperatures may limit its reproduction due to the high egg
1153 mortality observed at temperatures above 30°C (Table 2).

1154

1155 We suggest that the three traits related to population demography and thus invasiveness, namely
1156 voltinism, fecundity and hatching success, need to be recorded in a standardised unit so that
1157 population dynamics can be estimated from matrix population models. Furthermore, the trade-offs
1158 between, and rates of adaptation in, life-history traits are of intrinsic theoretical value (e.g. the trade-
1159 off between these three demographic traits among populations in different environments) and colour
1160 polymorphism of *H. axyridis* (Table 2) is also an interesting model system in population genetics.
1161 Overall, we suggest that the strength of biotic interactions centralised around *H. axyridis* (i.e. diet
1162 preference and foraging efficiency) and the three demographic traits are key variables for
1163 monitoring/assessing its performance and impact in invaded ecosystems.

1164

1165 The reproduction success of individual females has been measured in variable ways in *H. axyridis*
1166 according to regions (Table 2). Usually reproduction is measured as lifetime fecundity (total number
1167 of eggs laid by female), but this requires very long breeding and observation, since many females of
1168 *H. axyridis* live and reproduce for over four months (Awad et al. 2013). Alternatively, fecundity during

1169 the first month of reproduction (beginning by the day of the first egg laying, not including pre-
1170 oviposition period) is used. Both measures require feeding the females *ad libitum* with a suitable prey.
1171 Widely used types of prey that may become a standard are the pea aphid *Acyrtosiphon pisum* (Harris)
1172 (Hemiptera: Aphididae) and frozen eggs of the flour moth *E. kuehniella* (Berkvens et al. 2010a; Kögel
1173 et al. 2012). Other measures of reproductive performance could include daily fecundity (after a
1174 standard time period for example two weeks after the start of egg laying) and cluster size (again after
1175 a standard time period and perhaps an average over two weeks).

1176

1177 Fertility is defined as the product of fecundity and hatching rate. Hatching rate (percentage of eggs
1178 that hatch to the first larval instar) should be calculated over the first month of reproduction, since it
1179 declines strongly later (Awad et al. 2013). Hatching rate in *H. axyridis* in different countries varied from
1180 15% in Belgium (Berkvens et al. 2008) to 100% in Italy (unpublished data), although it has not been
1181 measured in most countries (Table 2). Hatching success may depend on many factors for example
1182 food source, colour morph, endosymbionts and multiple fertilisation. Thus permanent presence of
1183 one or more males with each female is recommended.

1184

1185 *Colour forms*

1186 More than 200 colour patterns of *H. axyridis* elytra have been observed in the native range (China),
1187 but most of them can be categorized into four major colour forms (Du, Chen 2010; Tang et al. 2012) .
1188 Controlled crossing experiments have shown that the majority of color patterns are controlled by 15
1189 alleles at one locus with multiple alleles (Komai 1956). However, all but four of these alleles are rare
1190 in natural populations, with a combined frequency of less than one per cent. The four major alleles
1191 are *succinea*, *axyridis*, *conspicua*, *spectabilis*, all but the first of these being melanic forms (Michie et
1192 al. 2010): 1) yellow to red background colour of elytra with the number of black dots ranging from 0
1193 to 19 (f. *succinea*); 2) black background colour of elytra with many orange-red dots (of varying size and
1194 position) (f. *axyridis*); 3) black background of elytra with one large orange-red dot in the top-centre of
1195 each elytron (f. *conspicua*); 4) black background colour of elytra with two orange-red dots on each
1196 elytron and the top one larger than the bottom one (f. *spectabilis*). The impressive diversity of colour
1197 patterns documented in China has been attributed to the diverse environmental conditions in the
1198 region as well as to complex interaction between rare allelic forms (Tan 1946). A hierarchical
1199 dominance with respect to phenotype expression was demonstrated between the four major colour
1200 alleles: *conspicua* > *spectabilis* > *axyridis* > *succinea* (Michie et al. 2010; Tan, Li 1934; Tan 1946). More
1201 specifically, the expression of the colour pattern in the heterozygous individuals (i.e. individuals
1202 bearing two different allelic forms) conforms to the rule of mosaic dominance heredity, which states

1203 that any portion of the elytra which has black pigment in the homozygote for a given allele will have
1204 black pigment also in the heterozygotes in which that allele is present (Tan 1946). Interestingly,
1205 Michie, Mallard et al. (2010) reported that the non-melanic morph *succinea* dramatically increases its
1206 degree of melanization at cold temperatures, and that there is genetic variation in reaction norms,
1207 with different families responding to temperature in different ways. The exact genomic architecture
1208 and gene content of the multiallelic locus controlling color morph variation and phenotypic plasticity
1209 of the non-melanic morph remains unknown.

1210

1211 In some of the earliest research in population genetics, the frequencies of these alleles were found to
1212 vary hugely across the native range of *H. axyridis* (Dobzhansky 1933). The geographical variation
1213 appeared to be linked to climate, with the non-melanic form *succinea* being found most often in hot,
1214 arid regions and melanic forms being more frequent in cooler, more humid ones (Dobzhansky 1933).
1215 This might be considered as a consequence of climatic adaptation. However, a different pattern was
1216 found in Japan, where *succinea* decreases in frequency from northeast to south-west without any
1217 significant correlation to temperature or other climatic factors (Komai 1956). Moreover, in north China
1218 f. *succinea* dominates, whereas in south China the melanic colour forms dominate (Du, Chen 2010;
1219 Tang et al. 2012). In addition to this geographic variation, small to large seasonal changes in allele
1220 frequencies have been reported in some native populations (Jiang et al. 2007; Osawa, Nishida 1992;
1221 Tang et al. 2012)). For example, in Beijing over half the population is melanic in the spring, but this
1222 drops to less than one-fifth by the autumn. Therefore, the melanic individuals presumably have a large
1223 fitness advantage in the winter and a disadvantage in the summer. This has been attributed to the
1224 effects of thermal melanism, with melanism being costly in summer and beneficial in winter, possibly
1225 mediated by mate choice (Wang et al. 2009).

1226

1227 The range of colour forms is limited within the invaded range. Indeed in most invaded regions only
1228 the non-melanic morph f. *succinea* is present, except in Europe where the melanic morphs f. *conspicua*
1229 and *spectabilis* are also present (and rarely f. *axyridis*), probably due to the genetic admixture with
1230 European biological control strains which occurred in this region (Lombaert et al. 2014; Lombaert et
1231 al. 2010). So far, it is not possible to say whether the predominance of f. *succinea* observed in the
1232 invaded range is due to historical and/or demographical contingencies (i.e. simple random effects) or
1233 to any selective process that would have favoured the establishment and the spatial spreading of f.
1234 *succinea*, for example the phenotypic plasticity of this morph (Michie et al. 2010). Geographical and
1235 seasonal variation of melanic and non-melanic morphs remains rather sparsely studied in Europe
1236 (Purse et al. 2014). In Belgium, the initial point of introduction of the species, the most commonly

1237 encountered morph is f. *succinea*, and the proportion of melanics (f. *spectabilis*, f. *conspicua*) is about
1238 25% (Adriaens et al. 2008). In this particular region of Europe, strong cold hardiness and differences
1239 in several fitness parameters between melanics and non-melanics from field populations have been
1240 demonstrated (Berkvens et al. 2008; Berkvens et al. 2010a).

1241

1242 *Natural enemies*

1243 Many regional reports have been published about one or several natural enemies of *H. axyridis* both
1244 within the native and invaded range but much could be revealed from a systematic approach
1245 comparing the native and invaded range (Table 1). There are a number of theories relating to IAS and
1246 their interactions with natural enemies but perhaps the most widely known is the Enemy Release
1247 Hypothesis (ERH) (Jeffries, Lawton 1984; Roy et al. 2011b; Roy, Lawson Handley 2012). The ERH
1248 predicts that an alien species introduced to a new region will increase in distribution and abundance
1249 because of reduced impacts from natural enemies. Adopting a 'biogeographical' (compare richness
1250 and impacts of enemies in native and introduced populations of an alien host) or 'community'
1251 (compare native and alien species occurring within the same community) approach for *H. axyridis*
1252 would be informative (Colautti et al. 2004). With both 'biogeographical' and 'community' approaches
1253 it is essential to consider how the loss of enemy diversity translates into population regulation. A small
1254 number of enemies may have large effects and so functional diversity of enemies may be a better
1255 predictor of impacts upon hosts than overall diversity. There is considerable scope for global
1256 collaboration in exploring *H. axyridis* within the context of ERH.

1257

1258 Generalist predators do attack ladybirds, for example sparrows have been confirmed as predators of
1259 *H. axyridis* in Slovakia (Veselý et al. in press), but parasites are the dominant natural enemies of
1260 ladybirds. Ladybirds are attacked by over 100 species of hymenopteran and dipteran parasitoids and
1261 several fungi (Ceryngier et al. 2012; Herz, Kleespiel 2012; Riddick et al. 2009). Of these, the majority
1262 of research globally has focused on the parasitoid *Dinocampus coccinellae* (Schrank) (Hymenoptera:
1263 Braconidae), which attacks both native and alien ladybirds (Ceryngier et al. 2012). *Dinocampus*
1264 *coccinellae* is a parasitoid of ladybirds that has a global distribution (Ceryngier et al. 2012) but currently
1265 the influence of alien ladybirds on the abundance and distribution of this parasitoid is unknown.
1266 Ladybirds vary in their quality as a host (Comont et al. 2014b; Koyama, Majerus 2008), but *D.*
1267 *coccinellae* does not discriminate between suitable and unsuitable ladybirds and will attack individuals
1268 differentially based on colour and movement (Cartwright et al. 1982; Obrycki et al. 1998; Richardson,
1269 Deloach 1972). Thus, the presence of unsuitable alien ladybird hosts such as *H. axyridis* may function
1270 as an ecological trap for the parasitoid, with positive effects on native ladybirds, or alternatively

1271 increase the abundance of the parasitoid, with adverse consequences for native ladybirds. It is
1272 apparent that *H. axyridis* is less susceptible to *D. coccinellae* than are other ladybirds (Berkvens et al.
1273 2010b; Comont et al. 2014b) but seems to be the most abundant and frequent *H. axyridis* parasitoid
1274 in many countries (Table 1) (Francati 2015a, b). Ongoing work is exploring the differences in immune
1275 response between *H. axyridis* and other ladybirds (Murray et al. 2015).

1276

1277 A semi-field study from the UK confirmed low rates of parasitism of *H. axyridis* by parasitoids,
1278 particularly in comparison to the native *C. septempunctata* (Comont et al. 2014b). Pupae of *H. axyridis*
1279 were parasitized, primarily by *P. fasciata* and *Phalacrotophora berolinensis* Schmitz (Diptera:
1280 Phoridae), at an exceptionally low level (1.73%) and adults were not found to be parasitized at all in
1281 this study; parasitism of the co-occurring *C. septempunctata* was high (20.91% pupae, 5.67% adults).
1282 Surveys in the Netherlands from 2003 revealed a number of natural enemies (*H. virescens*,
1283 *Parasitylenchus bifurcatus* Poinar & Steenberg (Nematoda: Allantonematidae), *Coccipolipus*
1284 *hippodamiae* and *Dinocampus coccinellae*) attacking *H. axyridis* but only from 2008 onwards (Raak-
1285 van den Berg, van Wielink et al. 2014) (Table 1). The suggestion is made that after a time lag of six
1286 years these natural enemies are starting to use *H. axyridis* as a novel host, following host shift from
1287 native ladybirds and adaptation to *H. axyridis*.

1288

1289 Recent research has demonstrated that *H. axyridis* individuals contain high numbers of obligate
1290 parasitic microsporidia (Vilcinskas et al. 2013). It appears that these microsporidia do not adversely
1291 affect *H. axyridis* but cause high mortality when artificially injected into *C. septempunctata* (Vilcinskas
1292 et al. 2013). Artificial injection, as used within this study to transmit the microsporidia from *H. axyridis*
1293 to *C. septempunctata*, is far removed from the natural mechanisms involved in microsporidia
1294 transmission (Solter et al. 2013), so further studies are required to explore the ecological relevance.
1295 Indeed further research is needed to understand how the presence of all established alien ladybirds
1296 influence parasitism and pathogen infection of declining native ladybirds.

1297

1298 The fungal pathogen *B. bassiana* commonly infects native species of ladybird (such as *C.*
1299 *septempunctata*), but again, *H. axyridis* seems highly resistant (Roy et al. 2008c). However, in Denmark
1300 several entomopathogenic fungi were isolated from overwintering and early season *H. axyridis*
1301 (larvae, pupae, adults) including *B. bassiana*, *Isaria farinosa* (Holmsk.) Fr. (Ascomycota:
1302 Cordycipitaceae), *Lecanicillium lecanii* (Zimm.) Zare & W. Gams (Ascomycota: Cordycipitaceae), and *L.*
1303 *muscarium* (Petch) Zare & W. Gams (Steenberg, Harding 2009a) (Table 1). Similarly, mid-summer
1304 surveys in Denmark of all *H. axyridis* life stages revealed infections from the same fungal assemblage

1305 with *I. farinosa* most prevalent, followed by *Lecanicillium* spp. (Howe, Ravn, Jensen, Meyling,
1306 unpublished data).

1307

1308 Additional work has assessed the sexually-transmitted ectoparasitic mite *Coccipolipus hippodamiae*
1309 (McDaniel & Morrill) (Acari: Podapolipidae) as a biological control candidate against *H. axyridis* (Roy
1310 *et al.* 2011c). This mite, which occurs naturally in Europe and North America (Table 1), causes sterility
1311 in female *H. axyridis*, but some native ladybird species are also susceptible to the mite, and thus it
1312 does not represent a suitable control strategy for *H. axyridis* (Rhule *et al.* 2010).

1313

1314 The obligate ectoparasitic fungus *H. virescens* has been capturing the imagination of a number of
1315 scientists working on *H. axyridis*. This species has historically received very little attention and so is of
1316 particular note. While most Laboulbeniales exhibit a high degree of host specificity, *H. virescens* has
1317 been reported from as many as 30 ladybird species in 17 genera (Bernardi *et al.* 2014; Ceryngier *et al.*
1318 2012; Ceryngier, Twardowska 2013; Haelewaters *et al.* 2012; Haelewaters *et al.* 2015b). Transmission
1319 of *H. virescens* occurs mainly during sexual contact, as exemplified by the non-random distribution of
1320 thalli on the body of males and females (Riddick *et al.* 2009; Welch *et al.* 2001); infection can be
1321 considered as a sexually transmitted disease (Welch *et al.* 2001). In *H. axyridis*, however, *H. virescens*
1322 is also socially transmitted; in overwintering aggregations, transmission of *H. virescens* through direct
1323 physical contact is the most important mechanism of spread (Nalepa, Weir 2007; Riddick 2006).
1324 Infection is caused by grooming, resulting in high thallus densities on older hosts (Haelewaters *et al.*
1325 2012). *Hesperomyces virescens* was reported for the first time on *H. axyridis* in Ohio in summer 2002
1326 (Garcés, Williams 2004). *Harmonia axyridis* is multivoltine, promiscuous, and overwinters in
1327 aggregations, all of which contribute to the rapid spread of *H. virescens* and higher infection
1328 prevalence on this host, compared to other ladybird hosts (De Kesel 2011). Interestingly, the parasite
1329 prevalence of *H. virescens* on *H. axyridis* varies between locations and between years (Haelewaters *et*
1330 *al.* 2012; Raak-van den Berg *et al.* 2014). In Belgium, for example, an increase from 0.5% to 96.5% of
1331 parasite prevalence was noted after only four years (De Kesel 2011). Currently, *H. virescens* infection
1332 of *H. axyridis* is widespread in Western Europe, the eastern United States and to a lesser extent in
1333 South Africa (D. Haelewaters unpublished). *Hesperomyces virescens* has also been reported on *H.*
1334 *axyridis* in its native range with one record from China, (Haelewaters *et al.* 2014). Ongoing work is
1335 assessing the influence of (dual) fungal infections on *H. axyridis* and *Olla v-nigrum* (Mulsant), a North
1336 American native ladybird species (Haelewaters *et al.* 2015a).

1337

1338 There is clearly much to uncover about the interactions between *H. axyridis* and natural enemies;
1339 global collaborations will provide unique opportunities for exploring these on biogeographic scales.

1340

1341 **Conclusions and future directions**

1342 *Harmonia axyridis* has inspired global collaborations and has also been the impetus for understanding
1343 biological invasions within and between countries. Many countries have documented the distribution
1344 and noted the rapid spread of *H. axyridis* following establishment. Further research is required to
1345 improve our understanding of the factors involved in determining the global patterns of invasion by
1346 *H. axyridis* which will have wide relevance for invasion biology. Many countries have engaged
1347 members of the public in monitoring the distribution of *H. axyridis* and the lessons learnt from such
1348 initiatives have been shared and proved informative for developing approaches to citizen science
1349 (Gardiner et al. 2012; Pocock et al. 2015; Roy et al. 2012a) and inspiring new projects both within and
1350 between countries. Indeed the role of volunteers in monitoring IAS is recognised (Roy et al. 2015b)
1351 and there is considerable scope to share resources and technology (August et al. 2015) to increase
1352 involvement in monitoring ladybirds and other IAS around the world.

1353

1354 The interactions between *H. axyridis* and other species have fascinated ecologists both in the native
1355 and invaded ranges of this species. There has been considerable focus on the potential impacts of *H.*
1356 *axyridis* on biodiversity, particularly intra-guild interactions and specifically IGP. Competitive
1357 interactions have received less attention but are worthy of future research emphasis. There is still
1358 much to unravel about the interactions between *H. axyridis* and its natural enemies. Comparisons
1359 between the native and invaded range will be particularly fruitful. Molecular studies have provided
1360 insights into genetic aspects of invasion and there is certainly more that can be revealed from detailed
1361 studies at a global scale. It is exciting to consider the potential of ongoing research to sequence the
1362 genome of *H. axyridis* and consider the opportunities that this research might present for future
1363 studies (Chown et al. 2015) ([http://www.agence-nationale-recherche.fr/?Project=ANR-13-EBID-](http://www.agence-nationale-recherche.fr/?Project=ANR-13-EBID-0001)
1364 [0001](http://www.agence-nationale-recherche.fr/?Project=ANR-13-EBID-0001)).

1365

1366 Many of the studies examining the interactions between *H. axyridis* and other species have involved
1367 mesocosm experiments under laboratory conditions. There is a need to increase the scale of such
1368 studies to consider the negative and positive ecosystem-level impacts of *H. axyridis*. *Harmonia axyridis*
1369 contributes pest control services in a number of crop systems but there is a lack of evidence in relation
1370 to ecosystem function and resilience of invaded systems. New molecular methods provide
1371 opportunities for detailed studies on the interactions between *H. axyridis* and the diverse range of

1372 species with which it interacts. Ecological network analysis represents an appealing and exciting way
1373 to explore these complex communities (Roy, Lawson Handley 2012). The coupling of citizen science
1374 approaches with global collaborations between researchers will provide the scale of information
1375 required to address some of the complex ecological questions that remain unanswered.

1376

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1401

1402

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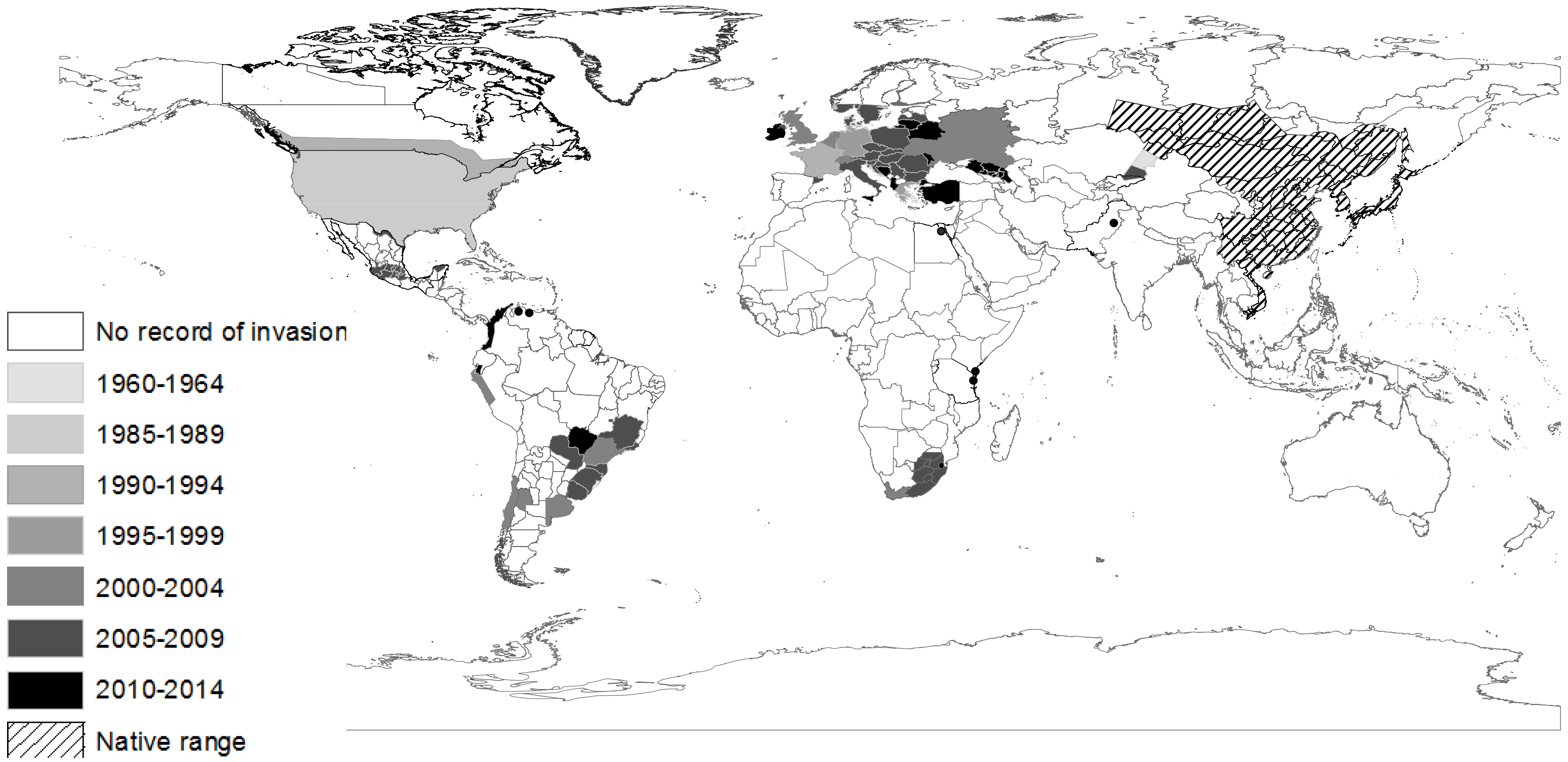
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- 2125 Figure 1 Global distribution of *Harmonia axyridis*.
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Legend

Harmonia_Europe

No record of invasion

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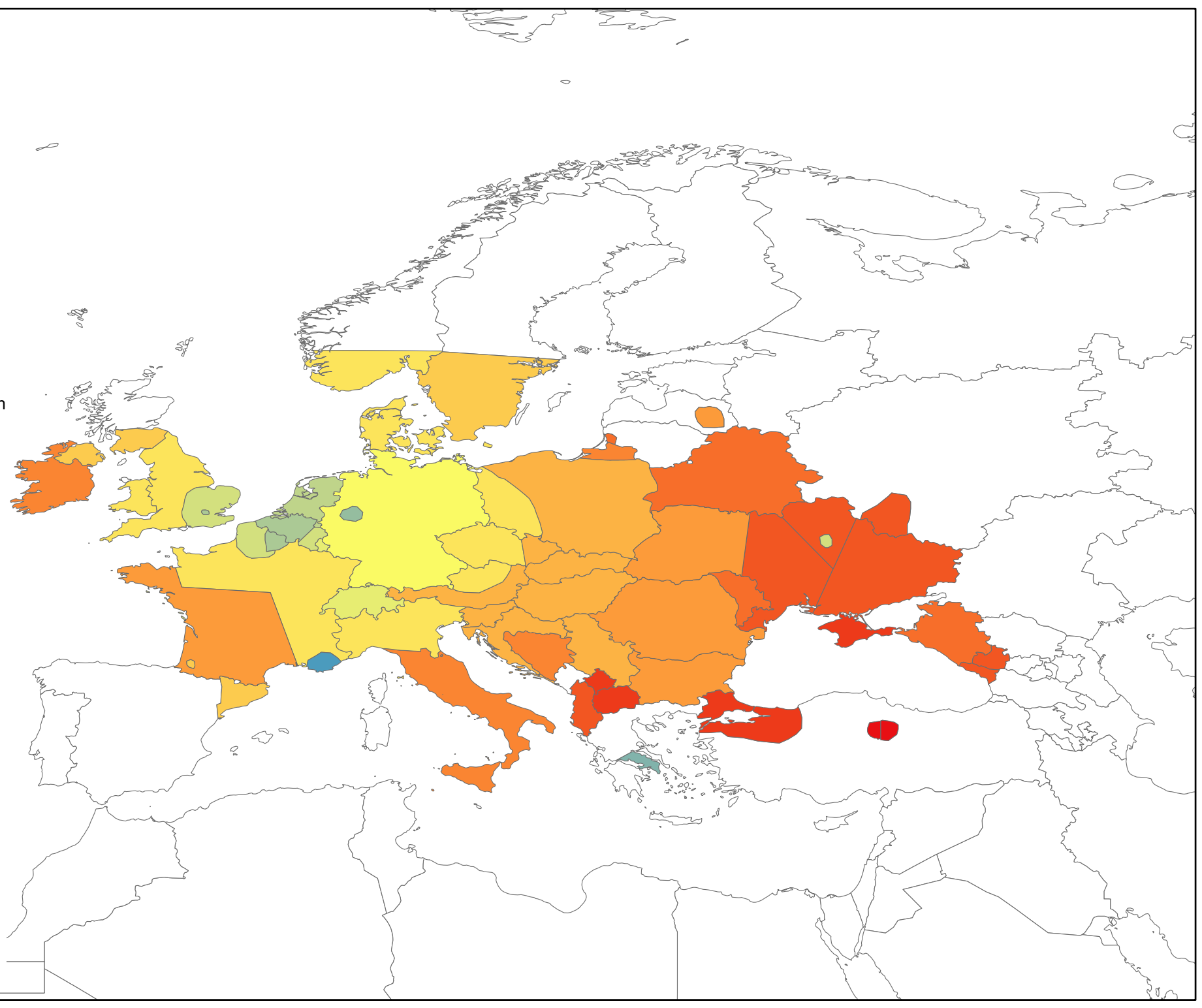


Table 1: Invasion characteristics and ecological attributes of *Harmonia axyridis* documented from countries around the world. It is important to note that various approaches have been adopted for categorising the attributes and so direct comparison between countries is not always possible. Standard 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), *Eucallipterus tiliae* (L.); Araneidae: *Araneus diadematus* Clerck (*Chrysoperla carnea* (Stephens) (Chrysopidae); *Homalotylus flaminus* (Dalman) (Encyrtidae); *Medina separata* (Meigen) (Tachinidae); *Metcalfa pruinosa* (Say) (Flatidae); *Oomyzus scaposus* (Thomson) (Eulophidae); *Passer montanus* (L.) (Passeridae)

	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	<i>Braconidae</i> <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/year. Expansion to the central regions is not yet known.	Wide Urban habitats Forests Fields Gardens Floodplains	Wide Aphids Coccids Psyllids Coccinellids	Unknown
North America	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/year	Wide Agricultural Woodlands Grasslands Residential and urban landscapes	Wide Many phytophagous 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>

South America (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>
Belgium	Intentional introduction as biocontrol agent in 1997	First wild population found in 2001	Range expansion of 189% on average per year (2002 to 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
Germany	Intentional introduction during end of 1990s. Unclear, if invasive populations derives from intentional introductions or spread.	Considered established since 2002	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 viticolae</i> Pollen	<i>Hesperomyces virescens</i> <i>Dinocampus coccinellae</i> Allantonematidae

					Fruit sap (e.g. from grape berries)	
Italy	<p>Intentional introductions from 1995 to 1999.</p> <p>Presumed that wild populations originated from biocontrol releases or secondary spread from France, Switzerland and other parts of Italy</p>	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	<p>Agricultural</p> <p>Gardens</p> <p>Vineyards</p> <p>Orchards</p>	<p>Wide</p> <p>Aphids</p> <p>Psyllids</p> <p>Coccids</p> <p><i>Metcalfa pruinosa</i></p> <p>Pollen</p>	<p><i>Dinocampus coccinellae</i></p> <p><i>Phalacrotophora fasciata</i></p>
The Netherlands	<p>Intentional introduction</p> <p>Presumed secondary spread from Belgium</p>	Found on outdoor crops in 1996 but first specimen (a pupa) in the wild recorded on 2002	Expanded from the first record in 2002 to spread rapidly from 2004 onwards, from south to north. By 2006 establishment across the entire country	<p>Agricultural (dominant in corn)</p> <p>Urban</p> <p>Predominantly on trees and shrubs but also on herbs in urban and anthropogenic habitats, less abundant in (semi-) natural areas</p>	<p>Wide</p> <p>Including cannibalism (observation of specimens egg-eating while other specimen was laying eggs)</p>	<p><i>Araneus diadematus</i> (autumn),</p> <p><i>Coccipolipus hippodamiae</i> (winter),</p> <p><i>Dinocampus coccinellae</i> (summer, winter)</p> <p><i>Hesperomyces virescens</i> (summer, winter)</p> <p><i>Parasitylenchus bifurcatus</i> (winter)</p> <p><i>Phalacrotophora fasciata</i> and</p> <p><i>Phalacrotophora</i> sp. (spring, summer)</p>

Norway	<p>Unintentional introduction</p> <p>Oslo in 2006, arrived as a stowaway on horticultural plants, <i>Thuja</i> sp. (Cupressaceae) imported from the Netherlands</p>	Late 2007 and throughout 2008 several adults were found indoors in the urban and suburban areas of Oslo	Limited to urban and suburban regions, and not recorded from commercial crops or in natural habitats	<p>Urban Gardens Parks</p> <p>Most records from the wider Oslo area. No reports from agricultural or horticultural crops</p>	Not measured	<i>Dinocampus coccinellae</i>
Slovakia	<p>Unintentional introduction.</p> <p>Presumed secondary spread from Austria, Poland and the Czech Republic</p>	First recorded in 2008	Expanded from the first record in 2008 across the entire country by 2009 at a rate of about 200km per year. Local topography played a role in the spread	<p>Urban Orchards Deciduous and lowland pine forests Vineyards Agricultural</p>	<p>Wide</p> <p>Hemiptera Larvae of Lepidoptera Dying flightless adults of Diptera</p>	<i>Chrysoperla carnea</i> <i>Passer montanus</i>
Switzerland	<p>Unintentional introduction</p> <p>Presumed secondary spread from Germany and France</p>	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	<p>Urban Woodland</p> <p>(particularly on broadleaved trees in woodlands and urban areas, but much less frequent on conifers, meadows or in agricultural habitats)</p>	Not measured	Not recorded

UK	<p>Unintentional introduction</p> <p>Presumed secondary spread from mainland Europe particularly Belgium and France</p>	<p>First recorded in 2003 and as established in 2005</p>	<p>Expanded from first record in 2003 at more than 100km per year in the UK, both via flight and anthropogenic transport</p>	<p>Urban Parks and gardens Woodlands (mainly deciduous) Grasslands Agricultural</p>	<p>Wide</p> <p>Hemiptera Lepidoptera Coleoptera</p>	<p><i>Dinocampus coccinellae</i> <i>Hesperomyces virescens</i> <i>Homalotylus flaminus</i> <i>Medina separata</i> <i>Oomyzus scaposus</i> <i>Phalacrotophora berlinensis</i> <i>Phalacrotophora fasciata</i> (Lower susceptibility of <i>H. axyridis</i> compared to other species evident from laboratory and field studies)</p>
South Africa	<p>Intentional introduction c. 1980: no establishment.</p> <p>Present invasion likely from unintentional introduction (unknown whether multiple).</p> <p>Eastern North America (genetic analysis of 4 South African populations)</p>	<p>First records 2001 (museum records). Established by 2006</p>	<p>Spread rapidly, established largely in cooler and more mesic regions. Initial spread of up to 500 km per year likely human-assisted.</p>	<p>Gardens (urban and rural) Orchards (deciduous and subtropical fruit) Vineyards Field crops Pine plantations Indoors Untransformed fynbos, grassland, moist savanna</p> <p>Frequently on oak trees, ornamental conifers, garden roses</p>	<p>Wide</p> <p>Field observations include: Aphids Coccinellids</p>	<p><i>Dinocampus coccinellae</i> <i>Hesperomyces virescens</i></p>

Table 2: Life history traits of *Harmonia axyridis* documented from countries around the world. 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 (μ l) or mass (mg). Voltinism 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 ($^{\circ}$ C), accumulated temperature (degree-days), lower lethal temperature ($^{\circ}$ C), lower lethal time (weeks), development time (days), maximum and minimum critical temperature (CTmax and CTmin respectively) ($^{\circ}$ C). Unless otherwise stated mean \pm standard error are given for all traits.

	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 \pm 0.46 (mean \pm SD) Lifetime: 1063.02 \pm 62.15 (mean \pm SD)	84.85 \pm 0.46%	Development threshold: 10.5 $^{\circ}$ C; cannot develop above 34 $^{\circ}$ C Accumulated temperature: 231.3 degree-days
Japan	Egg: volume 0.25 \pm 0.04 μ l (mean \pm SD) Adult female: size 6.73 \pm 0.53 mm (n=1106) (mean \pm SD) Adult male: size 6.16 \pm 0.43 mm (n=813)	<i>succinea</i> <i>spectabilis</i> <i>conspicua</i> <i>axyridis</i>	2–3	Clutch size: 39.11 \pm 1.47 Lifetime: 455.4 \pm 163.46	65.84 \pm 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.	1–3	Clutch size: 11–52	Not measured	Mating at 16–18 $^{\circ}$ C. Optimal temperature for egg development: 17–26 $^{\circ}$ C; for larval development: 26–

		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.				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
North America (USA)	Adult: length 4.8–7.47 mm, width 3.9–5.89 mm Egg: 0.25±0.0mg Adult male: 31.6±0.9mg Adult female: 53.6±2.2mg	Mainly <i>succinea</i> ; melanitic <i>H. axyridis</i> uncommon	2 plus a partial third	Clutch size: single eggs to more than 20 per cluster (> 60% of 3,149 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.

South America (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: 6–8.3mm); width 5.6±0.06 mm (range: 4.7 – 6.2 mm) Adult male: length 6.7±0.04mm (range: 5.5 – 7.7mm), width 5.3±0.05mm (range: 4.1 – 5.8mm)	<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 between 8.6–27.2°C. No eggs hatched at 33°C
Belgium	Adult: length 5–9 mm (median =7)	<i>succinea spectabilis</i> <i>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
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;	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: 1,174 eggs (max. 2,497)	82%	High egg and larval mortality at 33°C; LDT 11°C, SET 175 DD

	(migrating) males: 30.0±5.3 mg					
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.</i> <i>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 (%)
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 5.1mm, 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	<p>Adult female: length 5.8–8.0 mm (median = 7.0); width 4.8–6.5 mm (median = 5.4) (n = 37)</p> <p>Adult male: length 5.4–7.5 mm (median = 6.7); width 4.6–5.9 mm (median = 5.1) (n = 39)</p>	<i>succinea spectabilis 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 (particular temperature) assumed to be important
South Africa	<p>Adult female: length 6.9±0.1 mm (n=10); mass 35.3±1.0 mg (n=34)</p> <p>Adult male: length 6.3±0.1 mm (n=10); mass 29.1±0.9 mg (n=31)</p>	<i>succinea</i> with variation in spot number and background colour	Exact number unknown but at least 2	<p>Over 70 days: 245 ± 40 eggs</p> <p>Rearing conditions: 25/18°C (18h day/ 6h night cycle; 14hL/10hD photoperiod)</p>	<p>53±6.5% (n=650)</p> <p>Rearing conditions: 25/18 °C (18h day/ 6 night cycle; 14hL/10hD photoperiod)</p>	<p>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;</p> <p>Rearing conditions: 25/18°C (18h day/ 6h night cycle; 14hL/10hD photoperiod)</p>