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123 **Abstract**

124 The harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to Asia but
125 has been intentionally introduced to many countries as a biological control agent of pest insects. In
126 numerous countries, however, it has been introduced unintentionally. The dramatic spread of *H.*
127 *axyridis* within many countries has been met with considerable trepidation. It is a generalist top
128 predator, able to thrive in many habitats and across wide climatic conditions. It poses a threat to
129 biodiversity, particularly aphidophagous insects, through competition and predation, and in many
130 countries adverse effects have been reported on other species, particularly coccinellids. However,
131 the patterns are not consistent around the world and seem to be affected by many factors including
132 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
136 alien species have provided mechanistic evidence alongside models explaining large-scale patterns
137 and processes. The involvement of citizens in monitoring this species in a number of countries
138 around the 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
146 history and ecology of *H. axyridis* globally with consideration of future research perspectives. We
147 reflect broadly on the contributions of such research to our understanding of invasion biology while
148 also informing policy and people.

149

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

151

152 **Introduction**

153 The harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to Asia and is
154 a polymorphic, eurytopic species with a broad dietary range (Roy, Brown 2015a). It was widely
155 introduced as a biological control agent of pest aphids, but has spread to many countries within
156 which it was not intentionally released (Brown et al. 2008a). The global invasion of *H. axyridis* has
157 been rapid (Brown et al. 2011b). Concerns about the adverse impact of *H. axyridis* particularly on
158 biodiversity but also to people have motivated research across the world. There have been a
159 number of reviews considering the biology and ecology of *H. axyridis* (Kenis et al. 2008; Koch 2003;
160 Koch, Galvan 2008; Majerus et al. 2006; Pell et al. 2008; Pervez, Omkar 2006; Roy, Brown 2015a;
161 Sloggett 2012) often from a regional perspective but this species has an almost global distribution.
162 Therefore, it is timely to provide a world overview of research and perspectives. Indeed, the
163 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
170 agent and an invasive alien species (IAS) has informed a range of applied ecological themes, from
171 risk 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
175 overview of interactions between *H. axyridis* and other species before exploring its current global
176 distribution. We document, on a regional basis, the occurrence and invasion history of *H. axyridis*
177 providing an insight into research priorities and knowledge gaps identified by scientists from around
178 the world. Finally we qualitatively explore the observed traits of *H. axyridis* from both the native and
179 invaded 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
184 insects around the world, beginning with the successful introduction of the vedalia ladybird, *Rodolia*
185 *cardinalis* (Mulsant) to citrus groves of California (Caltagirone, Doult 1989). *Harmonia axyridis* has a
186 wide diet breadth (reviewed by Hodek and Evans 2012) including many species of aphids, which are

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

194

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

209

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

221

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

236

237 Even though *H. axyridis* can be considered an effective biological control agent at least from the US
238 studies, the Insurance Hypothesis predicts that control will in the long term be better achieved with
239 a diverse array of natural enemies (Loreau et al. 2003). Since *H. axyridis* tends to depress the
240 diversity of coccinellid assemblages (see below), consistently effective biological control may be
241 threatened by the invasion of *H. axyridis*. Further research is needed to unravel the role of *H.*
242 *axyridis* as a biological control agent of insect pests. Comparison of aphid populations before and
243 after the arrival of *H. axyridis*, or among places with higher and lower abundances of *H. axyridis*, may
244 provide useful information in this respect. Importantly, landscape composition has been found to
245 influence the effectiveness of biological control by *H. axyridis* and other predators. Indeed, soybean
246 fields embedded within diverse landscapes receive a greater pest control service from aphid
247 predators than fields within simplified agricultural landscapes (Gardiner et al. 2009c) compared to
248 landscapes dominated by forests and grasslands where soybean field size was reduced (Woltz,
249 Landis 2014). Similar studies have been carried out in Chile, in regions where *H. axyridis* dominated
250 the aphidophagous communities and again it has been demonstrated that biological control was
251 related to landscape composition with benefits seen through positive associations with the
252 abundance of woodland and urban habitats, but not with fruit crops, in the landscape (Grez et al.
253 2014a).

254

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

256

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

279

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

289

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

302

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

311

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

318

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

320

321 The majority of research examining interactions between *H. axyridis* and other aphidophagous
322 species has focused on direct interference competition on other ladybirds, proposing that decline is

323 due to strong asymmetric IGP of eggs and larvae in favour of *H. axyridis* (Pell et al. 2008). This
324 hypothesis is supported by many laboratory and field cage studies around the world (Cottrell 2004;
325 Gardiner, Landis 2007; Hoogendoorn, Heimpel 2002; Katsanis et al. 2013; Roy et al. 2008b; Snyder et
326 al. 2004; Soares, Serpa 2007; Ware, Majerus 2008; Ware et al. 2009; Yasuda et al. 2004). Under open
327 field conditions in Ohio, USA, eggs of the exotic *H. axyridis* were subject to lower predation relative
328 to the eggs of native species (Smith, Gardiner 2013). However, out of 342 attacks, video surveillance
329 illustrated that only two were attributable to alien ladybirds (*H. axyridis* feeding on conspecific eggs).
330 Instead, a diverse guild of predators (dominated by Opiliones, Tettigoniidae and the native *C.*
331 *maculata*) were responsible for the majority of egg attacks (Smith, Gardiner 2013). Importantly, this
332 study accounted only for egg predation but alien and native ladybird species may compete directly
333 through consumption of other life stages. Other tools, such as alkaloid (defensive chemicals within
334 coccinellids) sequestration analyses, frass analysis, and PCR-based gut content analyses, have been
335 developed to quantify the actual extent of interference competition occurring among native and
336 alien species (Brown et al. 2015; Davidson, Evans 2010; Gagnon et al. 2011; Hautier et al. 2008;
337 Hautier et al. 2011; Sloggett et al. 2009; Thomas et al. 2013). For example, Hautier et al. (2011)
338 found that 20.5% of 590 *H. axyridis* larvae in Belgium tested positive for native ladybird alkaloids.
339 Thomas et al. (2013) detected the DNA of native ladybirds within *H. axyridis* in the UK, with 3.7-
340 22.7% of 156 *H. axyridis* found to have consumed native species over three years. Gagnon et al.
341 (2011) used molecular gut content analysis to illustrate that IGP among larval ladybirds in soybean
342 fields can be very high; 52.9% of sampled ladybirds contained the DNA of one or more other ladybird
343 species. PCR primers have been developed and used to track aphid and ladybird predation by *H.*
344 *axyridis* fourth-instar larvae collected in lime trees in Italy, and it was found that 7% of sampled
345 individuals contained the DNA of one of two native ladybird species (Rondoni et al. 2014).

346

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

357 that ants exhibit high levels of predation (Burgio et al. 2008a). Further research has demonstrated
358 the influence of many factors on IGP, including intrinsic (such as feeding history of the species) and
359 extrinsic (such as habitat complexity), and highlighted the importance of addressing such factors
360 when considering the ecological relevance and extent of IGP (Ingels et al. 2015).

361

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

363

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

377

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

379

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

390

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

399

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

401

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

416

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

425 considerable financial costs. Management tactics have been developed to mitigate such nuisance
426 problems (Kemp, Cottrell 2015).

427

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

443

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

453

454

455 **Global distribution and regional research priorities**

456 *Harmonia axyridis* has become one of the world's most widely distributed ladybirds (Figure 1) and is
457 now found on all continents except Antarctica and notably is absent from a few large countries such
458 as Australia. Outside of its native range (Asia), it has become very widely established in North

459 America, South America and Europe (Figure 2), and in limited parts of Africa. There is a small
460 distance between the western edge of the native range and the eastern edge of the invaded range
461 (see *Russia and adjacent countries* below), and it seems inevitable that these populations will meet
462 in the near future.

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

466

467 **Asia**

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

470

471 *China*

472 *Harmonia axyridis* has a wide geographical range in China, especially in the north (Wang et al.
473 2007a). Current research on *H. axyridis* in China is mainly focused on agricultural applications,
474 including the development of artificial diet for *H. axyridis* to maximise production of this species for
475 field release in augmentative biological control (Wang et al. 2007b). *Harmonia axyridis* has also been
476 used extensively for testing pesticides and specifically examining the sensitivity of natural enemies
477 to pesticides (Tang et al. 2014). There is also ongoing research on the genetics of *H. axyridis* colour
478 polymorphism, specifically how colour variation interacts with environmental factors.

479

480 *Japan*

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

486

487 *Asian part of Russia, Kazakhstan and Kyrgyzstan*

488

489 The northern part of the native range of *H. axyridis* occupies the south of Siberia and the Far East.
490 The type locality of the species is in Siberia (Pallas 1771). The geographical distribution and colour
491 variability of this species was first studied in the 1920s (Dobzhansky 1924). A recent map of the
492 native range has been compiled (Orlova-Bienkowskaja et al. 2015). *Harmonia axyridis* populations

493 west of Baikal Lake (in West Siberia and the western part of East Siberia) differ both genetically and
494 morphologically from those living east of Baikal (Lombaert et al. 2014; Lombaert et al. 2011;
495 Vorontsov, Blekhman 2001).

496

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

510

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

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

526 belt of European Russia (Belgorod and Lipetsk regions) (Orlova-Bienkowskaja 2013; Ukrainsky,
527 Orlova-Bienkowskaja 2014), but it is unknown if the species is established there.

528

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

536

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

540

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

552

553 **North America**

554 *Hamonia axyridis* was repeatedly introduced throughout the twentieth century to the USA with the
555 aim of establishing sustaining populations (Gordon 1985; Harmon et al. 2007; Koch et al. 2006b).
556 Intentional releases of *H. axyridis* include a number of states but notably California in 1916, and
557 multiple eastern states from 1978 to 1992 (Chapin, Brou 1991; Gordon 1985; McClure 1987;
558 Tedders, Schaefer 1994). *Harmonia axyridis* was first detected beyond intentional release sites in the
559 United States in 1988 in south-eastern Louisiana and eastern Mississippi (Chapin, Brou 1991). A

560 second, independent set of releases led to establishment in the 1980s in the Pacific Northwest
561 (LaMana, Miller 1996; Lombaert et al. 2014; Lombaert et al. 2010). It is unknown whether all
562 established populations resulted from these releases or from additional, accidental introductions.
563 Nonetheless by the mid-1990s, *H. axyridis* had been found across the country with detection reports
564 from 45 of the 48 contiguous states by 2007 (Dreistadt et al. 1995; Hesler et al. 2001; Krafur et al.
565 1997; LaMana, Miller 1996; Mizell III 2007) and most recently from Montana in 2009 (Foley et al.
566 2009) and Arizona in 2008 (Fothergill et al. 2010). *Harmonia axyridis* was first detected in Canada in
567 1994 (Coderre et al. 1995). Currently this species is found throughout most of North America north
568 of Mexico with Labrador, Saskatchewan, Alaska and Wyoming the only areas where it has not yet
569 been reported (Foley et al. 2009; Fothergill et al. 2010; Hicks et al. 2010; Koch et al. 2006b).
570 *Harmonia axyridis* is also established and widespread in Mexico (Brown et al. 2011b).

571

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

579

580 **South America**

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

586

587 *Chile*

588 In 1998, a flightless strain of *H. axyridis* was introduced from France to central Chile for biological
589 control in greenhouses, but those populations did not establish (Grez et al. 2010) (Table 1). In 2003,
590 large numbers of flying *H. axyridis* associated with aphids in poplar trees were reported near the
591 release sites. In 2008, surveys of ladybird populations in alfalfa revealed only one individual *H.*
592 *axyridis* (from a sample of approximately 90,000 ladybirds), but rapid population increase was
593 observed over the next two years in alfalfa and other habitat or crop types (Grez et al. 2010).

594 *Harmonia axyridis* is currently one of the two most abundant species in alfalfa fields in central Chile,
595 representing 50 - 90% of ladybirds (Grez et al. 2014a; Grez et al. 2014b). It is expanding into other
596 habitats, including native vegetation, such as sclerophyllous matorral, although at very low densities
597 (Grez et al. 2013). *Harmonia axyridis* is spreading toward southern Chile, colonizing regions with
598 colder climates. In contrast, few records are reported towards northern Chile, where the Atacama
599 Desert is probably acting as a barrier for its invasion. From its original distribution in 2010, covering
600 a range of 250 km (north to south) near Santiago, it has expanded its distribution to ~2600 km (north
601 to south), and from sea level to >3000 m a.s.l., with a north to south spread of approximately 160
602 km year⁻¹. Genetic analyses suggest that current Chilean populations come from the East North
603 America strain (Lombaert et al. 2014), representing an accidental introduction. Only f. *succinea* has
604 been found in Chile.

605

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

618

619 Spatial distribution models are also being developed to forecast the future distribution of *H. axyridis*
620 in the country. Chile is a long (4329 km) and narrow (180 km on average) country, isolated by the
621 Atacama Desert to the north, the Pacific Ocean to the west, and the Andes mountain range to the
622 east. The Chilean environment has strong latitudinal gradients in abiotic conditions, from the most
623 arid desert in the world in the North, followed by a semi-arid region, Mediterranean type
624 ecosystems in central Chile, the temperate rainforests toward the South, and the southernmost sub-
625 Antarctic ecosystems (Luebert, Plissock 2006). This gradient offers a unique opportunity to study how
626 climate modulates the distribution and abundance of this invasive alien species. Also, along this

627 gradient, a highly diverse native fauna of coccinellids (~115 species) (González 2008) offers a unique
628 opportunity to evaluate the possible changes of native communities after *H. axyridis* arrival.

629

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

636

637 **Europe**

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

645

646 *Austria*

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

653

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

659

660 *Belgium*

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

668

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

675

676 *Czech Republic*

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

685

686 *Denmark*

687 *Harmonia axyridis* was first recorded in Copenhagen 2006, and presumed to have arrived from
688 Germany (Brown et al. 2008a; Pedersen et al. 2008). In the following years the beetle spread within
689 the Greater Copenhagen area, becoming established across the island of Zealand. By 2007/8, its
690 spread continued westwards to the islands of Lolland, Langeland, Ærø, and in the east to Bornholm
691 (perhaps arriving from Poland or Germany) where populations are now established (Howe 2015;
692 Howe et al. 2015; Steenberg, Harding 2009b; Steenberg et al. 2009). By 2008, *H. axyridis* had
693 reached Jutland in the far west of Denmark (Steenberg et al. 2009). The most northern record to
694 date (latitude 57° N) was from produce in a supermarket, highlighting the potential for spread

695 through anthropogenic pathways. Data from Zealand indicates stable populations with *H. axyridis*
696 dominating ladybird assemblages where established. Greatest densities occur within urban areas of
697 central Copenhagen (Ravn and Howe, unpublished data).

698

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

706

707 *France*

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

723

724 IAS expanding their range provide unique opportunities to explore the effect of spatial spread on
725 life-history traits, making it possible to test for a spatial arrangement of dispersal abilities along the
726 expanding range (Phillips et al. 2007; Purse et al. 2014). Moreover, the question of the evolution of
727 dispersal capacity in invasive populations is highly relevant, because it may accelerate spread, with
728 serious applied and theoretical consequences (Phillips et al. 2010; Travis, Dytham 2002). Using

729 controlled experiments in laboratory conditions, clear evidence was found of a strong, rapid increase
730 in flight speed with range expansion of *H. axyridis* from the core of the invaded area in Western
731 Europe (Belgium) to the front of this invaded area in South and Western parts of France (Lombaert
732 et al. 2014). This shift towards a higher flying speed at the invasion front was remarkably rapid, as it
733 was demonstrated after only eight years of expansion, corresponding to about 16 generations (Koch
734 2003).

735

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

758

759 In addition to the single vast admixed population which invaded Western Europe, a genetically
760 distinct population established in South East of France has been identified (Lombaert et al. 2014).
761 This population was first observed in 2005, and it appeared to have originated exclusively from the
762 European biological control strain introduced into Europe from 1982. This is surprising, at first sight,

763 because European biological control individuals have long been thought to be unable to survive in
764 the wild (Ferran et al. 1997). In support of this, it is apparent that this distinct population does not
765 seem to have expanded spatially, unlike most of the other *H. axyridis* outbreaks known all over the
766 world. This locally established population might attest, however, to the ability of the European
767 biological control strain to found small overwintering populations in the wild, in areas with clement
768 winters.

769

770 *Germany*

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

779

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

782

783 *Italy*

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

792

793 Research studies in Italy have focused on *H. axyridis* biology (Bazzocchi et al. 2004) and specifically
794 life table parameters. Research on the occurrence of parasitoids attacking *H. axyridis* is ongoing
795 (Francati 2015a, b; Rondoni et al. 2013a; Rondoni et al. 2013b). Other studies are focusing on the
796 development of a liver-based artificial diet, which could assist in maintenance of cultures of adult *H.*

797 *axyridis* (Sighinolfi et al. 2008), and on the susceptibility of *H. axyridis* larvae to lambda-cyhalothrin
798 insecticide (Benelli et al. 2015).

799

800 *Norway*

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

805

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

810

811 Observations in areas some distance from Oslo, such as Tvedestrand in Aust-Agder County (2008),
812 Våle in Vestfold County (2008) and Trondheim (2009) (the latter about 600 km north of Oslo)
813 revealed further spread or separate introduction to new areas (Sæthre et al. 2010). Repeated
814 introductions (probably on imported plants) are likely to be the most important factor for
815 introduction of the species to new areas in Norway. Natural geographic barriers and long distances
816 within Norway limit the species possibilities for rapid natural dispersal. However, anthropogenic
817 spread facilitates dispersal and of particular note was the occurrence of between 2000 and 3000
818 adult *H. axyridis* in a cargo of timber imported to Åndalsnes (Møre og Romsdal County) in March
819 2008 from Pennsylvania, USA. Some specimens were also recorded at Snåsa (Nord-Trøndelag
820 County) on the imported timber which was transported from Åndalsnes. According to the importing
821 timber company, actions had been taken to eradicate the beetles.

822

823 In late 2008 a website was launched to engage the public in submitting observations on-line and this
824 has made a major contribution to documenting the distribution of *H. axyridis* in Norway (Sæthre et
825 al. 2010). Records are available at

826 <http://www.artsportalen.artsdatabanken.no/#/Harmonia+axyridis/7468>. In autumn 2015 high
827 numbers of *H. axyridis* were reported from overwintering aggregations across the city of Oslo.
828 However, so far, the distribution of *H. axyridis* in Norway appears to be limited to urban and
829 suburban regions, and it has to date not been recorded or reported in commercial crops or in natural

830 habitats. Further studies on the biology, ecology, cold tolerance and winter survival will contribute
831 to better predictions of the dispersal and establishment potential of *H. axyridis* in Scandinavia.

832

833 *Slovakia*

834 *Harmonia axyridis* was first recorded in Slovakia in 2008 (Majzlan 2008). It arrived as an
835 unintentional introduction by secondary spread, following the spread across Austria (Rabitsch, Schuh
836 2006), Poland (Przewozny et al. 2007) and the Czech Republic (Špyňar 2008). There was less than
837 one year between the first record of establishment and widespread occurrence of *H. axyridis*. By the
838 end of 2009, it was recorded across Slovakia, and by the end of 2012 it occurred in numerous
839 habitats, particularly gardens, orchards and urban areas. The records from 2008–2012 document the
840 invasion clearly (Panigaj et al. 2014). The distribution and time sequence of the records support the
841 maximum rate of the spread of *H. axyridis* to be approximately 200 km year⁻¹, the spread being
842 accelerated by human movement (Panigaj et al. 2014). The local topography played a crucial role in
843 the spread: 47% of the records of the coccinellid were from lowlands (94–200 m), 36% from low hilly
844 areas (200–400 m), 11% from moderate altitudes (400–600 m) and only 6% from higher areas (600–
845 1250 m a.s.l.) (Panigaj et al. 2014). Despite great efforts in 2013 and 2014, only a single specimen of
846 *H. axyridis* was recorded from altitudes above 1000 m.

847

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

854

855 *Switzerland*

856 The first *H. axyridis* adult was found in 2004 in Basel (Klausnitzer 2002), but it was only in 2006 that
857 establishment was confirmed in several locations (Eschen et al. 2007). From then, the ladybird
858 rapidly invaded all areas of low and middle altitudes within two years. A long-term inventory was
859 initiated in the northwest of Switzerland in 2006 to record the impact of *H. axyridis* on native
860 ladybirds (Eschen et al. 2007). Ladybird populations were monitored using standardised sampling
861 methods at 45 sites: 15 broadleaved hedgerows, 15 meadows and 15 conifer sites several times a
862 year. The monitoring was interrupted only in 2014 but has since restarted. Other surveys were made
863 in other habitats on an irregular basis, in particular on urban trees. Since 2008, *H. axyridis* has

864 become by far the most abundant ladybird on broad-leaved shrubs and trees, accounting for 60 to
865 80% of all ladybirds collected throughout the year. In contrast, in meadows and on conifers, *H.*
866 *axyridis* still remains rather uncommon, except on some specific plants such as nettle (Kenis and
867 Eschen, unpublished data).

868

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

874

875 *The Netherlands*

876 *Harmonia axyridis* was first released as a biological control agent in greenhouses in 1995, on outdoor
877 crops, arboriculture and in urban areas since 1996, largely for the control of aphid pests (Cuppen et
878 al. 2004). Releases were stopped by the end of 2003. *Harmonia axyridis* has established at some
879 sites very rapidly with the first report of *H. axyridis* in the wild in 2002 in Groesbeek, Gelderland (as a
880 pupa on a leaf of *Hedera helix* L. (Araliaceae); Cuppen et al. 2004) followed by a specimen in
881 Rotterdam, South Holland in 2003, and around the same time another specimen was collected in
882 Reimerswaal, Zeeland. In July 2003 the first adult *H. axyridis* was collected on a lighted white sheet
883 at night at a nature reserve (De Kaaistoep, North Brabant) (Cuppen et al. 2004; van Wielink, Spijkers
884 2013). In this locality, up to 2014, 6516 specimens have been collected using light, 71.9% of which
885 were males (yearly range between 65 and 80%) (van Wielink, unpublished data).

886

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

897

898 Research in the Netherlands has focused on natural enemies (Haelewaters et al. 2012; Raak-van den
899 Berg et al. 2014; Sloggett 2010) and the high overwintering survival of *H. axyridis* (70.8-88.2%) (Raak-
900 van den Berg et al. 2012). The latter study found that overwintering survival was higher (1) at
901 sheltered places compared to exposed sites and (2) when ladybirds were overwintering at south-
902 western sides of buildings. As a comparison, winter survival of *A. bipunctata* in the Netherlands is
903 17-78% (Brakefield 1985).

904

905 *United Kingdom*

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

922

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

930

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

938

939 **Africa**

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

943

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

954

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

962

963 The introduction pathway of the contemporary invaders in South Africa is unknown, but all analysed
964 South African populations originated from eastern North America (Lombaert et al. 2014; Lombaert

965 et al. 2010). Introduction was likely unintentional, but it is unknown whether there was more than
966 one introduction to South Africa, disregarding the almost certainly failed introduction of the 1980s.

967

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

975

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

987

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

995

996 Research on *H. axyridis* in South Africa is scarce but it is recognised that there is a need to assess its
997 biology and ecology in order to evaluate its impact on native communities and agroecosystems.
998 Researchers from the Centre for Invasion Biology, Stellenbosch University, are focusing on the

999 thermal biology and life history of *H. axyridis* in South Africa and compare this species' traits to those
1000 of native aphidophagous ladybirds. This information can highlight characteristics that promote the
1001 invasiveness of *H. axyridis* in southern Africa and provide data for modelling its potential spread
1002 within and beyond borders (Shinner 2014). The study of its behavioural responses and adaptation to
1003 climate variation will remain a focus in the years to come as well as modes and mechanisms of
1004 introduction and range expansion investigated using molecular techniques.

1005

1006 However, many research aspects that are key for evaluating the establishment, spread and impact of
1007 *H. axyridis* are lacking. No systematic field surveys are taking place and therefore the invader's
1008 abundance across habitat types is also unknown. More importantly, data on the native ladybird
1009 communities (species richness and abundance) occurring in areas with and without *H. axyridis* are
1010 not being collected and the impacts on these communities are thus unknown. Of overriding
1011 importance may be the complete lack of baseline data prior to this invasion; it is possible that no
1012 readily comparable and uninvaded habitats may remain for urgent collection of baseline
1013 information. In addition, the taxonomy and phylogeny of the native Coccinellini need to be
1014 examined, in particular those African species currently placed in the genus *Harmonia*.

1015

1016 Under South African national legislation, *H. axyridis* is a Category 1b Listed Invasive Species
1017 (Department of Environmental Affairs South Africa 2014a), which in terms of the National
1018 Environmental Management: Biodiversity Act, 2004, legally is a "species which must be controlled"
1019 (Department of Environmental Affairs South Africa 2014b). How such control is to be achieved is
1020 unclear at present.

1021

1022 ***Failure of Harmonia axyridis to establish in some regions***

1023 *Harmonia axyridis* is much more commonly and widely distributed in the northern than in the
1024 southern hemisphere, perhaps unsurprising given its Asian origin. While *H. axyridis* distribution
1025 extends to boreal regions in its native range, its invasive distribution in the north and south of
1026 Europe, and also in northern Canada and Alaska, is more limited and suggests that climatic factors
1027 may be important in limiting the spread of this species. Globally, there are very few records from
1028 tropical regions (23.4°N–23.4°S); where it has been reported from the tropics it is not widely spread
1029 (e.g., Colombia, Venezuela, Kenya, Tanzania). In both South America and Africa, limits to its
1030 distribution apparently include warm tropical but also arid environments.

1031

1032 In Europe there are some habitats and regions that appear to be resistant to the establishment of *H.*
1033 *axyridis*. Some examples are the limited evidence of establishment in Greece (Kontodimas et al.
1034 2008), Turkey (Bukejs, Telnov 2015), Spain, including the Canary Islands (Goldarazena, Calvo 2007;
1035 Jacas et al. 2006; Pons et al. 2015), Bosnia and Herzegovina (Kulijer 2010), Portugal, including the
1036 Madeira and Azores archipelagos (Garcia 1986; Soares et al. 2008), Northern Ireland (Murchie et al.
1037 2008), the Republic of Ireland (<http://www.invasivespeciesireland.com>), and Réunion (Quilici, pers.
1038 com). It is as important to consider the regions in which *H. axyridis* has failed to establish as those in
1039 which it has succeeded. Only recently has consideration been given to understanding invasion
1040 failures within the context of invasion processes (Zenni, Nuñez 2013). The factors limiting invasion by
1041 *H. axyridis* in some geographic areas are worthy of exploration and could potentially provide insights
1042 into whether the southern and northern European ecosystems are more resilient to invasion than
1043 other parts of Europe and beyond. Investigation of equivalent patterns on the southern African
1044 subcontinent would also be informative.

1045

1046 Records of successful breeding by *H. axyridis* are very limited in Scotland (Roy, Brown 2015b) and
1047 although climatic conditions are not thought to have been a barrier to the colonization and spread of
1048 *H. axyridis* in southern Britain, it is possible that climate has limited its abundance not only in
1049 northern England and Scotland (Brown et al. 2008b; Roy, Brown 2015b), but also Denmark
1050 (Steenberg, Harding 2009b) and further north throughout Scandinavia. The combination of lower
1051 temperatures and higher precipitation in Scotland compared to England could be limiting the
1052 distribution of *H. axyridis* within Scotland. The Orkney and Shetland Islands are considered
1053 climatically unsuitable for *H. axyridis* (Poutsma et al. 2008), and in support of this there have only
1054 been occasional records of adults, arriving on produce imported from the mainland, from these
1055 northern islands (Ribbands et al. 2009). There are no records of immature stages of *H. axyridis*, or
1056 other ladybird species, on these islands.

1057

1058 Although thousands of individuals of both f. *succinea* and f. *conspicua* have been released in the
1059 Azores (Garcia 1986; Schanderl et al. 1992), *H. axyridis* has not become established there (Evans et
1060 al. 2011; Soares et al. 2008). It has been hypothesised that prey features related to local plant
1061 habitats and landscape structure, together with the ladybird characteristics in terms of body size,
1062 might explain why the invader is absent (Hemptinne et al. 2012). The coastal terrestrial habitats that
1063 form 9% of the landscape are the richest in terms of food resources for aphidophagous ladybirds. It
1064 is predicted that other large and medium-sized species of ladybirds (*Coccinella undecimpunctata* L.),
1065 which have requirement for high prey consumption, will also decline because of shortage of prey

1066 (Borges et al. 2006; Cabral et al. 2006; Sebastião et al. 2015; Soares et al. 2001) for example *C.*
1067 *septempunctata* is considered extinct from the Azores. The Azorean communities are nowadays
1068 dominated by minute Scymnini species and larger species are no longer recorded. Despite the
1069 competitive advantage of *H. axyridis* against the native *C. undecimpunctata* (Felix, Soares 2004; Nóia
1070 et al. 2008), it is apparent that Azorean habitat characteristics and the high feeding rate of *H.*
1071 *axyridis* are hampering its invasion.

1072

1073 **Comparison of traits**

1074 There have been a number of studies examining the influence of life-history traits on invasion and *H.*
1075 *axyridis* is no exception (Comont et al. 2014a; Comont et al. 2012). The traits databases compiled for
1076 these studies provides a rare opportunity to explore variation in life-history traits between localities
1077 (native and invaded) around the world. Extending and combining traits databases to a global scale
1078 will provide intriguing insights. The invasion process and ecological attributes (Table 1) and the
1079 compilation of life history traits of *H. axyridis* (Table 2) represents the start of this process and
1080 highlights gaps in understanding. However, qualitative comparisons of the traits of *H. axyridis* across
1081 the invaded range and with the native range reveals patterns that are worthy of further
1082 investigation.

1083

1084 *Habitat*

1085 The habitat of *H. axyridis* is wide and although poorly documented in many regions the exploitative
1086 and opportunistic nature of this species is evident (Table 1). During early stages of invasion it has
1087 been noted that *H. axyridis* is more prevalent within urban and agricultural landscapes than in semi-
1088 natural landscapes (Brown et al. 2008b; Grez et al. 2014a; Grez et al. 2014b). *Harmonia axyridis* is
1089 common within gardens and parks throughout the year and its presence in agricultural fields,
1090 orchards or vineyards has been documented globally and local damage due to quality loss of fruits is
1091 known (Koch et al. 2004a). Across Europe and Japan *H. axyridis* is commonly associated with trees
1092 and shrubs. For example in urban areas in Europe it is the most abundant ladybird on lime (*Tilia* spp.)
1093 and maple trees (*Acer* spp.) but is also frequently found on Scots pine, *Pinus sylvestris* L. (Pinaceae).
1094 The habitats of *H. axyridis* in Japan are disturbed areas such as agricultural fields, orchards, parks,
1095 residential yards and gardens (Osawa 2011) and *H. axyridis* is generally uncommon in natural forests
1096 (Osawa 2011).

1097

1098 In winter *H. axyridis* has a propensity to aggregate in buildings. Across Europe adults usually start
1099 aggregating in October and leave overwintering sites in April. The aggregating behaviour has been

1100 shown to depend on two blends of long chain hydrocarbon molecules, one leading conspecifics
1101 towards aggregation sites and the other ensuring cohesion of the aggregations (Durieux et al. 2012).
1102 These findings, with the identification of a volatile sex pheromone in female *H. axyridis* (Verheggen
1103 et al. 2007), might offer some potential in the development of specific control methods for *H.*
1104 *axyridis*.

1105

1106 It is critical that we have a better understanding of the habitat preference and suitability of *H.*
1107 *axyridis*; this is especially relevant when facing current global environmental change, especially
1108 urbanization, agricultural intensification and climate change which will undoubtedly affect the
1109 spread and distribution of *H. axyridis*. Habitat suitability could be estimated using Species
1110 Distribution Models based on fine-scale records on the presence/absence or densities of *H. axyridis*
1111 populations. Such results would have wide relevance to invasion biology.

1112

1113 *Diet breadth*

1114 The wide diet breadth of *H. axyridis* is evident from Table 1 and, as already stated, includes pest and
1115 non-pest insects but also fruits. Perhaps of most interest, and relevance to understanding the threat
1116 posed by this species to biodiversity, is the range of non-pest insects consumed and associated
1117 population-level effects. Much research has focussed on interactions between *H. axyridis* and other
1118 coccinellids (Pell et al. 2008) but there is a need for further work on other taxonomic groups for
1119 example expanding the research on butterflies such as the studies on the monarch butterfly *Danaus*
1120 *plexippus* (L.) (Koch et al. 2006a; Koch et al. 2003). Furthermore it is critical that future research
1121 considers the population-level effects of *H. axyridis* on different species and implications for
1122 ecosystem function. Current studies have not clearly documented the diet preference, adaptability
1123 and feeding efficiency of *H. axyridis*, which are essential for assessing its potential impact in recipient
1124 ecosystems.

1125

1126 *Thermal tolerance*

1127 Only a few studies, representing populations of *H. axyridis* from a few regions, have considered
1128 thermal tolerance (Table 2) (Koch et al. 2004b). Of particular importance would be to measure lower
1129 and upper temperature tolerance of several life stages using ecologically relevant conditions for the
1130 population examined. Indeed to build Species Distribution Models, thermal tolerance needs to be
1131 carefully measured in the laboratory so that the reaction norm of physiological/behavioural
1132 performance as a function of ambient temperature can be established. However, *H. axyridis* usually
1133 overwinters in shelters and aggregations and cold tolerance measurements should be interpreted in

1134 regards to ecologically relevant conditions. Indeed *H. axyridis* can be found at a range of altitudes: in
1135 Chile individuals have been found at >3000 m a.s.l. while in central Europe it is regularly present
1136 from the eastern lowlands (114 m a.s.l.) to montane/subalpine forests (approx. 1600 m a.s.l.,
1137 unpubl. data) in the Alps, with one isolated record of a probable wind-drifted individual at 2280 m
1138 a.s.l. in Carinthia.

1139
1140 Although laboratory studies show that invasive populations of *H. axyridis* do not survive at 34°C
1141 (Benelli et al. 2015), the species has been documented in Kenya (Nedvěd et al. 2011) and Tanzania
1142 (Nedvěd, Háva 2015) but there is no evidence that this species is abundant in the tropics. In addition,
1143 the wide spread and occurrence of *H. axyridis* in mesic cool climates or pockets of urban gardens
1144 within drier environments in its novel range suggests that climatic factors other than temperature
1145 may also play a role in shaping its distribution.

1146
1147 Desiccation resistance (Nedved, Kalushkov 2011) and the potential cross-effects of temperature and
1148 humidity on temperature limits may provide useful information for modelling its future distribution
1149 in face of climate change (Hoffmann et al. 2013). Perhaps more importantly, the study of the
1150 plasticity and evolutionary adaptation of tolerance limits in *H. axyridis* using both native and invasive
1151 populations would provide insights into its adaptive capacity to future climatic challenges. The effect
1152 of different climate regimes on the body weight and fat body content of *H. axyridis* and *C.*
1153 *septempunctata* has been the focus of laboratory studies in Germany (Krengel et al. 2012). This
1154 study concluded that that *C. septempunctata* has life history adaptations that would confer an
1155 advantage over *H. axyridis* at elevated temperatures.

1156
1157 *Reproductive potential*

1158 A number of traits (voltinism, fecundity and egg hatching success) reveal the high reproductive
1159 potential of *H. axyridis* (Table 2). In the native range, *H. axyridis* is generally considered to have two
1160 generations per year, although it can have three and occasionally up to eight generations in some
1161 years and localities (Osawa 2011). In Kyoto, in the centre of Japan, the overwintering adults mate
1162 and lay eggs in spring (Osawa 2000). The adults of the first generation emerge in mid May to June
1163 (Osawa 2000). In mid summer, the beetles aestivate in small groups in leaf-shelters on trees and the
1164 behaviour is regarded to be an adaptation to high temperature (Toda, Sakuratani 2006). In autumn,
1165 *H. axyridis* adults fly towards overwintering sites, white or pale objects on hilltops or valleys, where
1166 they aggregate from early November (Obata 1986).

1167

1168 Within much of the invaded range, *H. axyridis* only achieves two generations per year, whereas in
1169 the native range up to eight generations have been observed. Increases in global temperatures could
1170 facilitate an increase in voltinism, and corresponding increase in abundance across the invaded
1171 range in the future. On the contrary, increase in temperatures may limit its reproduction due to the
1172 high egg mortality observed at temperatures above 30°C (Table 2).

1173

1174 We suggest that the three traits related to population demography and thus invasiveness, namely
1175 voltinism, fecundity and hatching success, need to be recorded in a standardised unit so that
1176 population dynamics can be estimated from matrix population models. Furthermore, the trade-offs
1177 between, and rates of adaptation in, life-history traits are of intrinsic theoretical value (e.g. the
1178 trade-off between these three demographic traits among populations in different environments)
1179 and colour polymorphism of *H. axyridis* (Table 2) is also an interesting model system in population
1180 genetics. Overall, we suggest that the strength of biotic interactions centralised around *H. axyridis*
1181 (i.e. diet preference and foraging efficiency) and the three demographic traits are key variables for
1182 monitoring/assessing its performance and impact in invaded ecosystems.

1183

1184 The reproduction success of individual females has been measured in variable ways in *H. axyridis*
1185 according to regions (Table 2). Usually reproduction is measured as lifetime fecundity (total number
1186 of eggs laid by female), but this requires very long breeding and observation, since many females of
1187 *H. axyridis* live and reproduce for over four months (Awad et al. 2013). Alternatively, fecundity
1188 during the first month of reproduction (beginning by the day of the first egg laying, not including
1189 pre-oviposition period) is used. Both measures require feeding the females *ad libitum* with a suitable
1190 prey. Widely used types of prey that may become a standard are the pea aphid *Acyrtosiphon pisum*
1191 (Harris) (Hemiptera: Aphididae) and frozen eggs of the flour moth *E. kuehniella* (Berkvens et al.
1192 2010a; Kögel et al. 2012). Other measures of reproductive performance could include daily fecundity
1193 (after a standard time period for example two weeks after the start of egg laying) and cluster size
1194 (again after a standard time period and perhaps an average over two weeks).

1195

1196 Fertility is defined as the product of fecundity and hatching rate. Hatching rate (percentage of eggs
1197 that hatch to the first larval instar) should be calculated over the first month of reproduction, since it
1198 declines strongly later (Awad et al. 2013). Hatching rate in *H. axyridis* in different countries varied
1199 from 15% in Belgium (Berkvens et al. 2008) to 100% in Italy (unpublished data), although it has not
1200 been measured in most countries (Table 2). Hatching success may depend on many factors for

1201 example food source, colour morph, endosymbionts and multiple fertilisation. Thus permanent
1202 presence of one or more males with each female is recommended.

1203

1204 *Colour forms*

1205 More than 200 colour patterns of *H. axyridis* elytra have been observed in the native range (China),
1206 but most of them can be categorized into four major colour forms (Du, Chen 2010; Tang et al. 2012) .

1207 Controlled crossing experiments have shown that the majority of color patterns are controlled by 15

1208 alleles at one locus with multiple alleles (Komai 1956). However, all but four of these alleles are rare

1209 in natural populations, with a combined frequency of less than one per cent. The four major alleles

1210 are *succinea*, *axyridis*, *conspicua*, *spectabilis*, all but the first of these being melanic forms (Michie et

1211 al. 2010): 1) yellow to red background colour of elytra with the number of black dots ranging from 0

1212 to 19 (f. *succinea*); 2) black background colour of elytra with many orange-red dots (of varying size

1213 and position) (f. *axyridis*); 3) black background of elytra with one large orange-red dot in the top-

1214 centre of each elytron (f. *conspicua*); 4) black background colour of elytra with two orange-red dots

1215 on each elytron and the top one larger than the bottom one (f. *spectabilis*). The impressive diversity

1216 of colour patterns documented in China has been attributed to the diverse environmental conditions

1217 in the region as well as to complex interaction between rare allelic forms (Tan 1946). A hierarchical

1218 dominance with respect to phenotype expression was demonstrated between the four major colour

1219 alleles: *conspicua* > *spectabilis* > *axyridis* > *succinea* (Michie et al. 2010; Tan, Li 1934; Tan 1946).

1220 More specifically, the expression of the colour pattern in the heterozygous individuals (i.e.

1221 individuals bearing two different allelic forms) conforms to the rule of mosaic dominance heredity,

1222 which states that any portion of the elytra which has black pigment in the homozygote for a given

1223 allele will have black pigment also in the heterozygotes in which that allele is present (Tan 1946).

1224 Interestingly, Michie, Mallard et al. (2010) reported that the non-melanic morph *succinea*

1225 dramatically increases its degree of melanization at cold temperatures, and that there is genetic

1226 variation in reaction norms, with different families responding to temperature in different ways. The

1227 exact genomic architecture and gene content of the multiallelic locus controlling color morph

1228 variation and phenotypic plasticity of the non-melanic morph remains unknown.

1229

1230 In some of the earliest research in population genetics, the frequencies of these alleles were found

1231 to vary hugely across the native range of *H. axyridis* (Dobzhansky 1933). The geographical variation

1232 appeared to be linked to climate, with the non-melanic form *succinea* being found most often in hot,

1233 arid regions and melanic forms being more frequent in cooler, more humid ones (Dobzhansky 1933).

1234 This might be considered as a consequence of climatic adaptation. However, a different pattern was

1235 found in Japan, where *succinea* decreases in frequency from northeast to south-west without any
1236 significant correlation to temperature or other climatic factors (Komai 1956). Moreover, in north
1237 China *f. succinea* dominates, whereas in south China the melanic colour forms dominate (Du, Chen
1238 2010; Tang et al. 2012). In addition to this geographic variation, small to large seasonal changes in
1239 allele frequencies have been reported in some native populations (Jiang et al. 2007; Osawa, Nishida
1240 1992; Tang et al. 2012)). For example, in Beijing over half the population is melanic in the spring, but
1241 this drops to less than one-fifth by the autumn. Therefore, the melanic individuals presumably have
1242 a large fitness advantage in the winter and a disadvantage in the summer. This has been attributed
1243 to the effects of thermal melanism, with melanism being costly in summer and beneficial in winter,
1244 possibly mediated by mate choice (Wang et al. 2009).

1245

1246 The range of colour forms is limited within the invaded range. Indeed in most invaded regions only
1247 the non-melanic morph *f. succinea* is present, except in Europe where the melanic morphs *f.*
1248 *conspicua* and *spectabilis* are also present (and rarely *f. axyridis*), probably due to the genetic
1249 admixture with European biological control strains which occurred in this region (Lombaert et al.
1250 2014; Lombaert et al. 2010). So far, it is not possible to say whether the predominance of *f. succinea*
1251 observed in the invaded range is due to historical and/or demographical contingencies (i.e. simple
1252 random effects) or to any selective process that would have favoured the establishment and the
1253 spatial spreading of *f. succinea*, for example the phenotypic plasticity of this morph (Michie et al.
1254 2010). Geographical and seasonal variation of melanic and non-melanic morphs remains rather
1255 sparsely studied in Europe (Purse et al. 2014). In Belgium, the initial point of introduction of the
1256 species, the most commonly encountered morph is *f. succinea*, and the proportion of melanics (*f.*
1257 *spectabilis*, *f. conspicua*) is about 25% (Adriaens et al. 2008). In this particular region of Europe,
1258 strong cold hardiness and differences in several fitness parameters between melanics and non-
1259 melanics from field populations have been demonstrated (Berkvens et al. 2008; Berkvens et al.
1260 2010a).

1261

1262 *Natural enemies*

1263 Many regional reports have been published about one or several natural enemies of *H. axyridis* both
1264 within the native and invaded range but much could be revealed from a systematic approach
1265 comparing the native and invaded range (Table 1). There are a number of theories relating to IAS
1266 and their interactions with natural enemies but perhaps the most widely known is the Enemy
1267 Release Hypothesis (ERH) (Jeffries, Lawton 1984; Roy et al. 2011b; Roy, Lawson Handley 2012). The
1268 ERH predicts that an alien species introduced to a new region will increase in distribution and

1269 abundance because of reduced impacts from natural enemies. Adopting a 'biogeographical'
1270 (compare richness and impacts of enemies in native and introduced populations of an alien host) or
1271 'community' (compare native and alien species occurring within the same community) approach for
1272 *H. axyridis* would be informative (Colautti et al. 2004). With both 'biogeographical' and 'community'
1273 approaches it is essential to consider how the loss of enemy diversity translates into population
1274 regulation. A small number of enemies may have large effects and so functional diversity of enemies
1275 may be a better predictor of impacts upon hosts than overall diversity. There is considerable scope
1276 for global collaboration in exploring *H. axyridis* within the context of ERH.

1277

1278 Generalist predators do attack ladybirds, for example sparrows have been confirmed as predators of
1279 *H. axyridis* in Slovakia (Veselý et al. in press), but parasites are the dominant natural enemies of
1280 ladybirds. Ladybirds are attacked by over 100 species of hymenopteran and dipteran parasitoids and
1281 several fungi (Ceryngier et al. 2012; Herz, Kleespiel 2012; Riddick et al. 2009). Of these, the majority
1282 of research globally has focused on the parasitoid *Dinocampus coccinellae* (Schrank) (Hymenoptera:
1283 Braconidae), which attacks both native and alien ladybirds (Ceryngier et al. 2012). *Dinocampus*
1284 *coccinellae* is a parasitoid of ladybirds that has a global distribution (Ceryngier et al. 2012) but
1285 currently the influence of alien ladybirds on the abundance and distribution of this parasitoid is
1286 unknown. Ladybirds vary in their quality as a host (Comont et al. 2014b; Koyama, Majerus 2008), but
1287 *D. coccinellae* does not discriminate between suitable and unsuitable ladybirds and will attack
1288 individuals differentially based on colour and movement (Cartwright et al. 1982; Obrycki et al. 1998;
1289 Richardson, Deloach 1972). Thus, the presence of unsuitable alien ladybird hosts such as *H. axyridis*
1290 may function as an ecological trap for the parasitoid, with positive effects on native ladybirds, or
1291 alternatively increase the abundance of the parasitoid, with adverse consequences for native
1292 ladybirds. It is apparent that *H. axyridis* is less susceptible to *D. coccinellae* than are other ladybirds
1293 (Berkvens et al. 2010b; Comont et al. 2014b) but seems to be the most abundant and frequent *H.*
1294 *axyridis* parasitoid in many countries (Table 1) (Francati 2015a, b). Ongoing work is exploring the
1295 differences in immune response between *H. axyridis* and other ladybirds (Murray et al. 2015).

1296

1297 A semi-field study from the UK confirmed low rates of parasitism of *H. axyridis* by parasitoids,
1298 particularly in comparison to the native *C. septempunctata* (Comont et al. 2014b). Pupae of *H.*
1299 *axyridis* were parasitized, primarily by *P. fasciata* and *Phalacrotophora berlinensis* Schmitz (Diptera:
1300 Phoridae), at an exceptionally low level (1.73%) and adults were not found to be parasitized at all in
1301 this study; parasitism of the co-occurring *C. septempunctata* was high (20.91% pupae, 5.67% adults).
1302 Surveys in the Netherlands from 2003 revealed a number of natural enemies (*H. virescens*,

1303 *Parasitylenchus bifurcatus* Poinar & Steenberg (Nematoda: Allantonematidae), *Coccipolipus*
1304 *hippodamiae* and *Dinocampus coccinellae*) attacking *H. axyridis* but only from 2008 onwards (Raak-
1305 van den Berg, van Wielink et al. 2014) (Table 1). The suggestion is made that after a time lag of six
1306 years these natural enemies are starting to use *H. axyridis* as a novel host, following host shift from
1307 native ladybirds and adaptation to *H. axyridis*.

1308

1309 Recent research has demonstrated that *H. axyridis* individuals contain high numbers of obligate
1310 parasitic microsporidia (Vilcinskas et al. 2013). It appears that these microsporidia do not adversely
1311 affect *H. axyridis* but cause high mortality when artificially injected into *C. septempunctata*
1312 (Vilcinskas et al. 2013). Artificial injection, as used within this study to transmit the microsporidia
1313 from *H. axyridis* to *C. septempunctata*, is far removed from the natural mechanisms involved in
1314 microsporidia transmission (Solter et al. 2013), so further studies are required to explore the
1315 ecological relevance. Indeed further research is needed to understand how the presence of all
1316 established alien ladybirds influence parasitism and pathogen infection of declining native ladybirds.

1317

1318 The fungal pathogen *B. bassiana* commonly infects native species of ladybird (such as *C.*
1319 *septempunctata*), but again, *H. axyridis* seems highly resistant (Roy et al. 2008c). However, in
1320 Denmark several entomopathogenic fungi were isolated from overwintering and early season *H.*
1321 *axyridis* (larvae, pupae, adults) including *B. bassiana*, *Isaria farinosa* (Holmsk.) Fr. (Ascomycota:
1322 Cordycipitaceae), *Lecanicillium lecanii* (Zimm.) Zare & W. Gams (Ascomycota: Cordycipitaceae), and
1323 *L. muscarium* (Petch) Zare & W. Gams (Steenberg, Harding 2009a) (Table 1). Similarly, mid-summer
1324 surveys in Denmark of all *H. axyridis* life stages revealed infections from the same fungal assemblage
1325 with *I. farinosa* most prevalent, followed by *Lecanicillium* spp. (Howe, Ravn, Jensen, Meyling,
1326 unpublished data).

1327

1328 Additional work has assessed the sexually-transmitted ectoparasitic mite *Coccipolipus hippodamiae*
1329 (McDaniel & Morrill) (Acari: Podapolipidae) as a biological control candidate against *H. axyridis* (Roy
1330 et al. 2011c). This mite, which occurs naturally in Europe and North America (Table 1), causes
1331 sterility in female *H. axyridis*, but some native ladybird species are also susceptible to the mite, and
1332 thus it does not represent a suitable control strategy for *H. axyridis* (Rhule et al. 2010).

1333

1334 The obligate ectoparasitic fungus *H. virescens* has been capturing the imagination of a number of
1335 scientists working on *H. axyridis*. This species has historically received very little attention and so is
1336 of particular note. While most Laboulbeniales exhibit a high degree of host specificity, *H. virescens*

1337 has been reported from as many as 30 ladybird species in 17 genera (Bernardi et al. 2014; Ceryngier
1338 et al. 2012; Ceryngier, Twardowska 2013; Haelewaters et al. 2012; Haelewaters et al. 2015b).
1339 Transmission of *H. virescens* occurs mainly during sexual contact, as exemplified by the non-random
1340 distribution of thalli on the body of males and females (Riddick et al. 2009; Welch et al. 2001);
1341 infection can be considered as a sexually transmitted disease (Welch et al. 2001). In *H. axyridis*,
1342 however, *H. virescens* is also socially transmitted; in overwintering aggregations, transmission of *H.*
1343 *virescens* through direct physical contact is the most important mechanism of spread (Nalepa, Weir
1344 2007; Riddick 2006). Infection is caused by grooming, resulting in high thallus densities on older
1345 hosts (Haelewaters et al. 2012). *Hesperomyces virescens* was reported for the first time on *H.*
1346 *axyridis* in Ohio in summer 2002 (Garcés, Williams 2004). *Harmonia axyridis* is multivoltine,
1347 promiscuous, and overwinters in aggregations, all of which contribute to the rapid spread of *H.*
1348 *virescens* and higher infection prevalence on this host, compared to other ladybird hosts (De Kesel
1349 2011). Interestingly, the parasite prevalence of *H. virescens* on *H. axyridis* varies between locations
1350 and between years (Haelewaters et al. 2012; Raak-van den Berg et al. 2014). In Belgium, for
1351 example, an increase from 0.5% to 96.5% of parasite prevalence was noted after only four years (De
1352 Kesel 2011). Currently, *H. virescens* infection of *H. axyridis* is widespread in Western Europe, the
1353 eastern United States and to a lesser extent in South Africa (D. Haelewaters unpublished).
1354 *Hesperomyces virescens* has also been reported on *H. axyridis* in its native range with one record
1355 from China, (Haelewaters et al. 2014). Ongoing work is assessing the influence of (dual) fungal
1356 infections on *H. axyridis* and *Olla v-nigrum* (Mulsant), a North American native ladybird species
1357 (Haelewaters et al. 2015a).

1358

1359 There is clearly much to uncover about the interactions between *H. axyridis* and natural enemies;
1360 global collaborations will provide unique opportunities for exploring these on biogeographic scales.

1361

1362 **Conclusions and future directions**

1363 *Harmonia axyridis* has inspired global collaborations and has also been the impetus for
1364 understanding biological invasions within and between countries. Many countries have documented
1365 the distribution and noted the rapid spread of *H. axyridis* following establishment. Further research
1366 is required to improve our understanding of the factors involved in determining the global patterns
1367 of invasion by *H. axyridis* which will have wide relevance for invasion biology. Many countries have
1368 engaged members of the public in monitoring the distribution of *H. axyridis* and the lessons learnt
1369 from such initiatives **have been shared and proved informative** for developing approaches to citizen
1370 science (Gardiner et al. 2012; Pocock et al. 2015; Roy et al. 2012a) **and inspiring new projects both**

1371 within and between countries. Indeed the role of volunteers in monitoring IAS is recognised (Roy et
1372 al. 2015b) and there is considerable scope to share resources and technology (August et al. 2015) to
1373 increase involvement in monitoring ladybirds and other IAS around the world.

1374

1375 The interactions between *H. axyridis* and other species have fascinated ecologists both in the native
1376 and invaded ranges of this species. There has been considerable focus on the potential impacts of *H.*
1377 *axyridis* on biodiversity, particularly intra-guild interactions and specifically IGP. Competitive
1378 interactions have received less attention but are worthy of future research emphasis. There is still
1379 much to unravel about the interactions between *H. axyridis* and its natural enemies. Comparisons
1380 between the native and invaded range will be particularly fruitful. Molecular studies have provided
1381 insights into genetic aspects of invasion and there is certainly more that can be revealed from
1382 detailed studies at a global scale. It is exciting to consider the potential of ongoing research to
1383 sequence the genome of *H. axyridis* and consider the opportunities that this research might present
1384 for future studies (Chown et al. 2015) ([http://www.agence-nationale-recherche.fr/?Project=ANR-13-
1385 EBID-0001](http://www.agence-nationale-recherche.fr/?Project=ANR-13-EBID-0001)).

1386

1387 Many of the studies examining the interactions between *H. axyridis* and other species have involved
1388 mesocosm experiments under laboratory conditions. There is a need to increase the scale of such
1389 studies to consider the negative and positive ecosystem-level impacts of *H. axyridis*. *Harmonia*
1390 *axyridis* contributes pest control services in a number of crop systems but there is a lack of evidence
1391 in relation to ecosystem function and resilience of invaded systems. New molecular methods
1392 provide opportunities for detailed studies on the interactions between *H. axyridis* and the diverse
1393 range of species with which it interacts. Ecological network analysis represents an appealing and
1394 exciting way to explore these complex communities (Roy, Lawson Handley 2012). The coupling of
1395 citizen science approaches with global collaborations between researchers will provide the scale of
1396 information required to address some of the complex ecological questions that remain unanswered.

1397

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1422

1423

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- 2146 Figure 1 Global distribution of *Harmonia axyridis*.
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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	Braconidae <i>Medina luctuosa</i> <i>Phalacrotophora philaxyridis</i> <i>Hesperomyces virescens</i> <i>Strongygaster triangulifera</i> Birds
Japan	Native	Native	Native	Wide Urban habitats Parks Backyards Agricultural Gardens (mainly on trees and shrubs)	Wide Aphids Ladybird larvae	<i>Dinocampus coccinellae</i> <i>Phalacrotophora</i> sp.

Siberia and the Far East	Native	Native	Native	Wide Deciduous Coniferous forests Gardens Urban habitats Grasslands Fields	Wide Aphids Coccids Psyllids Coccinellids	Birds <i>Dinocampus coccinellae</i>
European Russia	Multiple intentional releases in the Caucasus starting in 1930s (not established). First population seen in wild in 2010 in the west. Invasive population likely secondary spread from Poland	Established in the west and in the south. Individual specimens found in centre of European Russia	Range expansion in the south estimated at 300 km/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 Fruit sap (e.g. from	<i>Hesperomyces virescens</i> <i>Dinocampus coccinellae</i> Allantonematidae

					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>	First recorded in 2003 and as established in 2005	Expanded from first record in 2003 at more than 100km per year in the UK, both via flight and anthropogenic transport	<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>	First records 2001 (museum records). Established by 2006	Spread rapidly, established largely in cooler and more mesic regions. Initial spread of up to 500 km per year likely human-assisted.	<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 (μl) 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 ($^{\circ}\text{C}$), accumulated temperature (degree-days), lower lethal temperature ($^{\circ}\text{C}$), lower lethal time (weeks), development time (days), maximum and minimum critical temperature (CT_{max} and CT_{min} respectively) ($^{\circ}\text{C}$). 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 $^{\circ}\text{C}$; cannot develop above 34 $^{\circ}\text{C}$ Accumulated temperature: 231.3 degree-days
Japan	Egg: volume 0.25 \pm 0.04 μl (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 $^{\circ}\text{C}$. Optimal temperature for egg development: 17–26 $^{\circ}\text{C}$; 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> ; melanic <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>

Legend

Harmonia_Europe

No record of invasion

- 1991
- 1994
- 1998
- 1999
- 2001
- 2002
- 2003
- 2004
- 2005
- 2006
- 2007
- 2008
- 2009
- 2010
- 2011
- 2012
- 2013
- 2014



