

The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion

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Abstract Released as a biological control agent of aphids and coccids, *Harmonia axyridis* (Coleoptera: Coccinellidae) has spread from Asia to four additional continents. Since 1988 *H. axyridis* has established in at least 38 countries in its introduced range: three countries in North America, six in South America, 26 in Europe and three in Africa. In different continents the species has spread at rates estimated between 100 and 500 km year⁻¹. Here, the

global spread of *H. axyridis* is thoroughly reviewed. Mechanisms of short- and long-distance dispersal in coccinellids are discussed, as are the reasons for them, with particular emphasis on *H. axyridis*. Dispersal via anthropogenic means has been particularly important in the case of *H. axyridis*. Preliminary studies investigating the invasion routes of *H. axyridis* using genetic analyses (involving both microsatellite and mitochondrial DNA) are outlined.

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This research was conducted as part of a collaboration of scientists working on *Harmonia axyridis*.

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Introduction

Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) is an organism that has induced hundreds of studies over many decades (Sloggett 2005). This beetle, with many vernacular names, including harlequin ladybird, multicolored Asian lady beetle and Halloween beetle, is of interest to biologists in several fields. Firstly, it is a highly polymorphic species, with variation in colour morphs evident across its range, and has thus long been a study species for geneticists (e.g. Dobzhansky 1933; Komai et al. 1950). Secondly, it is a large, voracious and resilient coccinellid and was therefore a target for use in biological control programs. Indeed, *H. axyridis*

has a long history of use as a classical biological control agent of aphids and coccids since 1916 (Gordon 1985). It has been widely used for pest control in crops as diverse as pecans (Teddners and Schaefer 1994) and red pines (McClure 1987). As a biological control agent, *H. axyridis* has incidentally succeeded in controlling pest aphid species on other crops, including apples (Brown and Miller 1998) and citrus fruits (Michaud 2002) and has had a pest-controlling role in other crop systems, including soybean, maize, alfalfa, tobacco, winter wheat and cotton (reviewed in Koch 2003; Koch and Galvan 2008). In Europe *H. axyridis* was released in a number of augmentative biological control programs (e.g. Trouvé et al. 1997; Adriaens et al. 2003; Coutanceau 2006). Thirdly, from its native range in Asia, *H. axyridis* has spread in four further continents at a very fast rate during the last 23 years (see below). This is of great interest to biologists studying range expansions of species, and specifically, invasions by alien species. Possible negative impacts of *H. axyridis* on native species have been a particular concern (Roy and Wajnberg 2008), with many studies focussing on the role of intraguild predation (Pell et al. 2008), though cannibalism may be even more important in maintaining *H. axyridis* dominance (Osawa 2011).

For all of these reasons, *H. axyridis* can be seen as a model organism, and many of the studies are no doubt of wide general interest, and not restricted to those researchers studying the Coccinellidae. In this paper we outline the global spread of *H. axyridis* and its current known distribution, the mechanisms behind that spread, and discuss genetic evidence of its invasion routes (using analyses of both microsatellite and mitochondrial DNA).

Global distribution of *H. axyridis*

Asia

Harmonia axyridis is native to China (range extending to the far south, e.g. Yunnan and Guangxi Provinces), Japan, Korea, Mongolia, and eastern Russia (Dobzhansky 1933; Kuznetsov 1997), although its entire native range has not been clearly recorded. In Russia, the species occurs at least as far north as Krasnoyarsk (southern Siberia) (Poutsma et al. 2008), as far west as the Altai Mountains and

Novosibirsk (Iablokoff-Khnzorian 1982) and the range extends to the eastern seaboard (through Amur region, Khabarovsk territory and Primorye territory) and beyond, to the islands of Sakhalin and Kuril (Kuznetsov 1997). Kuznetsov (1997) also reports the range to include northern Kazakhstan, and introductions of *H. axyridis* were made in that country, at least in the south-east (e.g. Alma-Ata) (Hodek 1973). However, studies of *H. axyridis* specimens from Kazakhstan indicate no obvious genetic differentiation from populations in the western part of the native range (E. Lombaert and A. Estoup, unpublished data; C. Thomas, unpublished data), suggesting that the species may be native to that country. Presence in Taiwan and the Himalayas was documented but is in doubt (Poutsma et al. 2008), in the former case because of possible misidentification with *Harmonia yedoensis* Takizawa.

North America

Harmonia axyridis of Japanese origin was first introduced in the USA (California and Hawaii) in 1916 (Iablokoff-Khnzorian 1982) (Table 1). However, despite many further releases, including at least fourteen in various states between 1964 and 1982 (Gordon 1985) *H. axyridis* was not reported as established in the country until 1988, in Louisiana (Chapin and Brou 1991). However, evidently the species then spread very quickly and by 1994 it was present in at least 24 states, including most states adjoining both the east and west coasts (Koch et al. 2006). *Harmonia axyridis* continued to be found in further states, and was recently recorded for the first time in Montana (2006) (Foley et al. 2009) and Arizona (2008) (Fothergill et al. 2010), leaving Wyoming and Alaska as the only states without a record of the species. *Harmonia axyridis* became established in Canada by 1994 (Coderre et al. 1995) and quickly spread across much of the southern part of the country (Majka and McCorquodale 2006). Having recently been recorded in Newfoundland (2009, although an earlier specimen from 2000 was also noted) (Hicks et al. 2010), the species has now been found in all but two jurisdictions (i.e. Labrador and Saskatchewan) (Hicks et al. 2010). *Harmonia axyridis* was introduced in Mexico as a biological control agent in the states of Chihuahua, Colima, and Yucatán (Koch et al. 2006). The species is

Table 1 The global distribution of *Harmonia axyridis*, listed by continent and country

Country	Year of first record in the wild (not necessarily established)	Deliberately introduced? (Earliest year of introduction)	Evidence of establishment?	References
Asia				
Russia (Eastern, S. Siberia), Mongolia, China, Japan and Korea	N/A (native range)	N/A	N/A	Dobzhansky (1933) and Kuznetsov (1997)
Kazakhstan	Unknown	Yes (1968)	Yes	Hodek (1973)
Georgia	Unknown	Yes (1927)	Unknown	Poutsma et al. (2008)
North America				
USA	1988	Yes (1916)	Yes	Chapin and Brou (1991)
Canada	1994	No	Yes	Coderre et al. (1995)
Mexico	Pre 2006	Yes (pre 2001)	Yes	Koch et al. (2006)
South America				
Argentina	2001	Yes (1986)	Yes	Saini (2004)
Brazil	2002	No	Yes	de Almeida and da Silva (2002)
Chile	2003	Yes (1998)	Yes	Grez et al. (2010)
Peru	2003	No	Yes	Grez et al. (2010)
Paraguay	2006	No	Yes	Silvie et al. (2007)
Uruguay	2009	No	Yes	Nedvéd and Krejčík (2010)
Colombia	2010	No	Unknown	J. Lundgren (personal communication)
Europe				
France	1991	Yes (1982)	Yes (2003)	Coutanceau (2006) and Ferran et al. (1997)
Greece	1998	Yes (1994)	Limited	Kontodimas et al. (2008)
Germany	1999	Yes (1997)	Yes	Tolasch (2002)
Belgium	2001	Yes (1997)	Yes	Adriaens et al. (2003)
Netherlands	2002	Yes (1996)	Yes	Cuppen et al. (2004)
England	2003	No	Yes	Majerus et al. (2006)
Switzerland	2004	Yes (1996)	Yes	Klausnitzer (2004)
Luxembourg	2004	No	Yes	Schneider and Loomans (2006)
Italy	2006	Yes (1990s)	Yes	Brown et al. (2008a) and Burgio et al. (2008)
Czech Republic	2006	Yes (2003)	Yes	Brown et al. (2008a)
Denmark	2006	Yes (2000s)	Yes	Brown et al. (2008a) and Steenberg and Harding (2009)

Table 1 continued

Country	Year of first record in the wild (not necessarily established)	Deliberately introduced? (Earliest year of introduction)	Evidence of establishment?	References
Austria	2006	No	Yes	Rabitsch and Schuh (2006)
Norway	2006	No	Yes	Staverløkk et al. (2007)
Poland	2006	No	Yes	Przewozny et al. (2007)
Wales	2006	No	Yes	Brown et al. (2008b)
Spain	2007	Yes (1995)	No	Goldarazena and Calvo (2007)
Liechtenstein	2007	No	Yes	Brown et al. (2008a)
N. Ireland	2007	No	No	Murchie et al. (2008)
Scotland	2007	No	Yes	Holroyd et al. (2008)
Sweden	2007	No	Yes	Brown et al. (2008a)
Croatia	2008	No	Yes	Stanković et al. (2010)
Hungary	2008	No	Yes	Merkl (2008)
Serbia	2008	No	Yes	Thalji and Stojanovic (2008)
Slovakia	2008	No	Yes	O. Nedvěd and V. Marko (personal communications)
Slovenia	2008	No	Yes	Bravničar et al. (2009)
Ukraine	2009	Yes (1964)	Yes	Marko and Pozsgai (2009)
Bulgaria	2009	No	Yes	Tomov et al. (2009)
Latvia	2009	No	Yes	Barševskis (2009)
Romania	2009	No	Yes	Marko and Pozsgai (2009)
Bosnia and Herzegovina	2010	No	No	Kulijer (2010)
Ireland	2010	No	No	http://www.invasivespeciesireland.com
Belarus	Unknown	Yes (1968)	Unknown	Sidlyarevich and Voronin (1973)
Portugal	None	Yes (1984)	No	
Africa				
South Africa	2001	No	Yes	Stals and Prinsloo (2007)
Egypt	Pre 2007	Yes (pre 2000)	Limited	Ferran et al. (2000)
Lesotho	2008	No	Yes	Stals (2010)
Kenya	2010	No	Limited	Nedvěd et al. (in press)
Tunisia	None	Yes	No	EPPO (2002)
Australia				
Australia	None, but imported specimens intercepted	No	No	Smith (2008)

widespread in Mexico. Koch et al. (2006) reported *H. axyridis* from five further states (where *H. axyridis* was not released)—Coahuila, Jalisco, Morelos, Puebla and Mexico State—and the species has since been found established in the southern-most state, Chiapas (O. Nedvěd, personal communication), which borders Guatemala.

South America

The first report of *H. axyridis* in South America came from Argentina (Saini 2004) (Table 1; Fig. 1a). The species was introduced as a biological control agent, first in Mendoza in 1986 (Poutsma et al. 2008) and was recorded in Buenos Aires (2001) (Saini 2004), Santa Fe (2004) (Montero and Vignaroli 2008) and Entre Rios (2008) (R. Stals, personal communication), so it appears to be widespread in the northern half of the country. The flightless biocontrol strain of *H. axyridis* (Tourniaire et al. 2000) was introduced in Chile in 1998 (Grež et al. 2010). There is no record of establishment at that time and the first report of the species in the wild is from 2003 (Los Andes, Valparaiso region), although with no further reports until recently (Grež et al. 2010). However, *H. axyridis* is clearly now established in central Chile, with 17 records (including larvae) in various localities and habitats in the Metropolitan and Valparaiso regions, as documented by Grež et al. (2010). The species is abundant in places; an aggregation of over 650 *H. axyridis* individuals was reported from an apartment in Santiago in May 2010 (Grež et al. 2010). As far as we know, *H. axyridis* was not deliberately released in Brazil but it has been recorded there in four regions—Paraná (2002) (de Almeida and da Silva 2002), São Paulo (2004) (Arruda Filho et al. 2009), Minas Gerais (2006) (Rezende et al. 2010) and Brasilia (2009) (Martins et al. 2009)—suggesting a northerly spread up the eastern side of the country. *Harmonia axyridis* is established in Paraguay, and appears to be widespread in the south of the country, with records from Caaguazú, Coronel Bogado and Caacupé (Silvie et al. 2007). The earliest record is from Caaguazú in 2006, and adults and larvae have been recorded in cotton crops there (Silvie et al. 2007). Present in Peru since 2003 (L. Valencia, personal communication), *H. axyridis* was reported from Lima and Tumbes (Grež et al. 2010), both of which are on the Pacific coast. The latter is very close

to the border with Ecuador. Apparently the species is established in Peru and is common in places (Grež et al. 2010). *Harmonia axyridis* is also reported to be present in western Colombia (Valle de Cauca) (J. Lundgren, personal communication). The latest South American country in which *H. axyridis* has been found is Uruguay, where it was recently reported as established (Nedvěd and Krejčík 2010). Records were from Canelones (adults found in late 2009, with larvae found at the same locality in early 2010), and Montevideo (2010) (Nedvěd and Krejčík 2010). Both of these localities are in the south of the country. *Harmonia axyridis* has clearly spread quickly in South America, and further countries seem likely to be invaded.

Europe

In Europe, early introductions of *H. axyridis* occurred in the east, including to Ukraine from 1964 (for control of aphids on fruit trees) (Katsoyannos et al. 1997) and Belarus from 1968 (Sidlyarevich and Voronin 1973). In western Europe, *H. axyridis* was first used as a biological control agent in 1982 in France and first marketed in 1995 (Coutanceau 2006), with various companies making the species commercially available (Adriaens et al. 2003). It established in the late 1990s and expanded its range rapidly, especially from 2002 (Brown et al. 2008a) (Table 1; Fig. 1b). The spread and distribution of *H. axyridis* in Europe is detailed in Brown et al. (2008a), who reported establishment in at least 13 European countries. However, the species has continued to spread rapidly and is now known to be established in 13 additional countries (Table 1). In the west there are recent (2010) first records from Ireland (although establishment there is yet to be confirmed) (<http://www.invasivespeciesireland.com>) and in the east the established range now includes Poland (2006) (Przewozny et al. 2007), Hungary (2008) (Merkl 2008), Slovakia (2008) (O. Nedvěd and V. Marko, personal communications), Latvia (2009) (Barševskis 2009), Romania (2009) (Marko and Pozsgai 2009) and Ukraine (2009) (Marko and Pozsgai 2009). In the south, Croatia (2008) (Stanković et al. 2010), Serbia (2008) (Thalji and Stojanovic 2008), Slovenia (2008) (Bravničar et al. 2009) and Bulgaria (2009) (Tomov et al. 2009) have established populations, and the species has recently been reported in

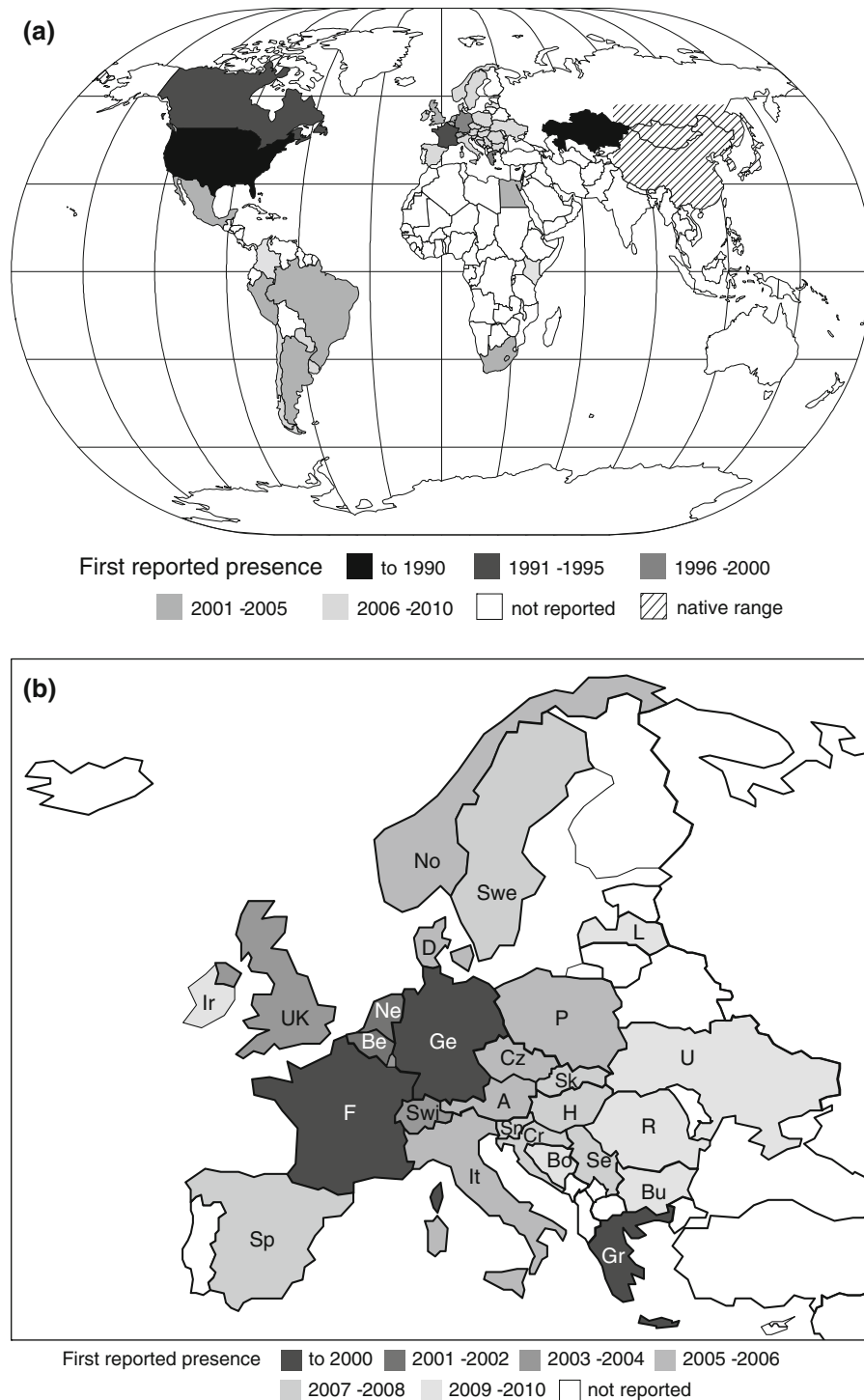


Fig. 1 The known distribution of *Harmonia axyridis* (based on confirmed reports of the species in the wild) up to and including 2010: **a** globally; **b** in Europe. *Note:* in most cases entire countries are coloured, but this does not mean that *H. axyridis* necessarily occurs throughout. *A* Austria, *Be* Belgium, *Bo* Bosnia

and Herzegovina, *Bu* Bulgaria, *Cr* Croatia, *Cz* Czech Republic, *D* Denmark, *F* France, *Ge* Germany, *Gr* Greece, *H* Hungary, *Ir* Ireland, *It* Italy, *L* Latvia, *Ne* Netherlands, *No* Norway, *P* Poland, *R* Romania, *Se* Serbia, *Sk* Slovakia, *Sn* Slovenia, *Sp* Spain, *Swe* Sweden, *Swi* Switzerland, *U* Ukraine, *UK* United Kingdom

Bosnia and Herzegovina (2010) (Kulijer 2010). The northern-most location in Europe where the species has been recorded is Trondheim, Norway (Saethre et al. 2010).

Africa

Harmonia axyridis was introduced in Tunisia (EPPO 2002) and Egypt (Ferran et al. 2000) (Table 1; Fig. 1a). The status of the species in northern Africa is largely unknown to us. However, *H. axyridis* may be established around Cairo, as reported by Brown et al. (2008a) and was recently still being released as a biological control agent in Egypt. In South Africa *H. axyridis* has been established since 2001, when it was recorded in Cape Town and Stellenbosch (Western Cape Province), with larvae and pupae present (Stals 2010). At first this went largely unnoticed, but since late 2006, when *H. axyridis* was found again in Western Cape Province, Riaan Stals has gradually been piecing together the spread of the species in South Africa (Stals and Prinsloo 2007; Stals 2010). Thus *H. axyridis* has now been recorded in all nine provinces, as follows: Western Cape (2001), Eastern Cape (2006), KwaZulu-Natal, Free State and Gauteng (all 2007–2008), Mpumalanga, Northern Cape, North-West Province and Limpopo (all 2009). The species is not thought to have been deliberately introduced in South Africa, and Stals (2010) hypothesises its arrival first to Western Cape Province via human transport (sea, air or road). Lesotho (a mountainous country entirely surrounded by South Africa) is the second country in southern Africa with confirmed reports of *H. axyridis*. The species is established there, having been discovered in June 2008, and was recorded at altitudes of up to 2500 m (Stals 2010). In 2010 *H. axyridis* was found on the east coast of Kenya (Kikambala) and may be established there (Nedvěd et al. in press), indicating tolerance to a tropical climate. *Harmonia axyridis* may well be present, but unreported, in other regions of Africa.

Australia

Harmonia axyridis is not known to be established in the continent of Australia. However, there are documented examples of the species arriving in Australia. It was inadvertently imported with excavation equipment to Bunbury (Western Australia) in

2008, but all specimens were dead (Smith 2008), and about 20 *H. axyridis* (some live and pupating) were intercepted at Darwin (Northern Territory), having arrived by air from the USA in 2009 (Carvan 2009).

Predicted global distribution

Poutsma et al. (2008) provided very useful predictions of the potential distribution of *H. axyridis* based on climate modelling. The subsequent observed spread of the species so far conforms to these predictions. We propose that the eastern edge of the European range of *H. axyridis* will continue to expand and may eventually meet the western edge of the Asian range, thus giving a more-or-less continuous distribution across the Palearctic, from Ireland in the west to Japan in the east. There is little scope for further range expansion in North America, as Alaska and northern Canada are climatically unsuitable for the species and almost all other regions have already been invaded. In South America, Venezuela, Ecuador and Bolivia are suitable for the species from a climatic viewpoint—and all of these share borders with countries that already have *H. axyridis*. Whilst Amazonia may be unsuitable for *H. axyridis*, much of the remainder of South America is suitable for invasion. Very large areas of southern and eastern Africa (including Madagascar) and the coastal belt of northern Africa are also climatically suitable for the species. Whilst invasion risk is likely to be lessened by a combination of geographic isolation and rigorous import procedures, New Zealand and coastal Australia (excluding northern regions) are climatically suitable for *H. axyridis* (Poutsma et al. 2008). In summary, there are clearly further vulnerable ecosystems beyond the current known distribution that are potentially under threat of invasion by *H. axyridis*. In the long term on a global scale, it may only be northerly and southerly latitudes, high altitudes, desert regions, and some tropical regions, that escape invasion.

Habitat use by *H. axyridis*

Harmonia axyridis is generally stated in the literature to be semi-arboreal (Hodek 1973), but it occupies many habitats, and in parts of both its native and introduced ranges has been recorded in meadows,

heathlands and riparian zones (Adriaens et al. 2008), reed beds (Ware et al. 2005) and crop systems (Colunga-Garcia and Gage 1998; Jansen and Hautier 2008). *Harmonia axyridis* has been recorded on fruit trees in many countries. Indeed, some of the earliest records of the species in several countries were from fruit trees, e.g. Italy (peach and citrus) (Burgio et al. 2008), Denmark (apple and *Prunus* sp.) (Steenberg and Harding 2009), Hungary (apple and pear) (Marko and Pozsgai 2009), Latvia (orchard trees) (Barševskis 2009) and São Paulo, Brazil (citrus) (Arruda Filho et al. 2009). In the review by Koch et al. (2006), *H. axyridis* in North America is reported from 40 plant species, including three *Malus* spp. (apple), two *Prunus* spp. (peach and plum) and *Citrus* spp. Thus it is evident that fruit trees are to some extent targeted by *H. axyridis* as a feeding habitat, either because of the aphid and coccid prey that the trees harbour, or because of the fruit itself, which *H. axyridis* may feed on (Kovach 2004). Feeding on grapes has been a particular focus of attention, as if harvested with *H. axyridis*, about one beetle per kg of fruit is enough to taint the wine (Linder et al. 2009). This has caused concern in North America (Galvan et al. 2008), Europe (Linder et al. 2009) and South Africa (Stals 2008).

In Great Britain, verified records of *H. axyridis* collected via a public engagement survey (<http://www.harlequin-survey.org>) were analysed in terms of broad habitat categories. Taking 2008 as an example, the species was found in the following habitats: 1. built up areas and gardens (53.4% of the 1298 × 1 km² with records of *H. axyridis*); 2. grassland (20.4%); 3. arable and horticultural land (19.6%); 4. woodland (5.5%) (P. Brown, unpublished data). These data, presented at coarse summary resolution here, are biased in terms of both the density of human population (affecting record submission) and the relative land areas of each habitat in Great Britain, but illustrate the generalist nature of *H. axyridis* habitat use. Deciduous trees and shrubs dominated in terms of plant use by *H. axyridis* in this study, with the majority of such records coming from built up areas and gardens, rather than from woodland. *Harmonia axyridis* was recorded as occurring on at least 75 families of flowering plant, with 50 families recorded with larvae present, suggesting a very broad range of suitable plants for *H. axyridis* in Great Britain (P. Brown, unpublished data). Adriaens et al. (2008) reported similar results from Belgium.

Six of the seven biomes of South Africa (Grassland, Savanna, Fynbos, Forest, Thicket and Nama Karoo) have records of *H. axyridis*, which has been recorded from sea level up to altitudes of at least 1800 m. The exception is the very arid Succulent Karoo biome that dominates in the north-west of South Africa. Although many reports were from urban locations, the species was also found in natural habitats, including unspoilt fynbos (Cape maquis) and pristine grassland, and large populations have been recorded in important wine production areas of Western Cape Province (Stals 2010). In Brazil, *H. axyridis* was recently reported from tropical semi-deciduous forest (Milleo et al. 2008). Also in Brazil, 38 plant species (from 18 families) were recorded with the presence of *H. axyridis* (Martins et al. 2009), further illustrating the versatility of the species. *Harmonia axyridis* forms large overwintering aggregations, and in its invaded range these tend to be in or on buildings, e.g. North America (Koch and Galvan 2008) and Europe (Brown et al. 2008a). The resulting nuisance factor of the beetles indoors is also a problem in at least parts of the native range of *H. axyridis*, e.g. Northeast China (Wang et al. 2011).

In summary, whilst it is evident in all invaded continents that *H. axyridis* has a tendency to thrive in anthropogenic habitats (both urban and agricultural), it is also able to establish in a wide range of natural and semi-natural habitats. Continued negative impacts of *H. axyridis* on native species through intraguild predation and competition (e.g. Brown et al. 2011a) are predicted. Thus it is likely that biodiversity in important ecosystems, especially in Africa and South America, may suffer negative effects, if, as seems likely, *H. axyridis* continues to thrive and expand in its invaded range.

Investigating the invasion routes of *H. axyridis* using genetic analyses

Inferring invasion routes is an essential step towards implementing control measures and understanding the success of an invasive species (Estoup and Guillemaud 2010). As discussed above, observational records have proved useful for mapping the spread of an invasive species (Brown et al. 2008b), but molecular genetic approaches provide additional, unique insights into invasion dynamics, and allow

specific hypotheses to be tested. For example, were there several independent introductions of individuals from the native area into the invasive range? Or was there a stepping stone colonisation process, involving a single introduction from the native range into the invasive range, followed by subsequent invasions occurring from within the invasive range (e.g. Estoup and Guillemaud 2010)? It is generally expected that an introduced population will have low genetic diversity, and therefore reduced potential for adaptation to a new environment. However, multiple introductions are common during invasions by many taxa, e.g. plants (Kang et al. 2007), reptiles (Kolbe et al. 2004), molluscs (Facon et al. 2003), crustaceans (Kelly et al. 2006), and insects (Fonseca et al. 2000; Miller et al. 2005; Ciosi et al. 2008) (and see Lawson Handley et al. (2011), for a review). This can lead to combinations of novel genotypes that could increase genetic diversity in the invasive relative to native ranges, particularly if source populations are highly differentiated (e.g. Kolbe et al. 2004; Dlugosch and Parker 2008). This is particularly the case for species with wide geographical ranges, which are more likely to be successful invaders (Theoharides and Dukes 2007), and could be pertinent to *H. axyridis*. In addition to source populations and invasion routes, data generated in molecular studies can be used to infer the number of founders, and the genetic characteristics of the founding population, giving insights into the mechanisms underlying a successful invasion.

We recently investigated the global invasion routes of *H. axyridis* using neutral molecular markers (18 microsatellites) in populations from across the native Asian range (eight populations from Japan, China, South Korea, Kazakhstan and Russia), from biocontrol companies (Biobest and Biotop) and from the invasive range (five populations from North America, Europe, South America and South Africa) (Lombaert et al. 2010). The invasive populations represent the initial invasive population found in each invaded area. We performed traditional genetic analyses, and a modern Approximate Bayesian Computation (ABC) method implemented in DIYABC (Cornuet et al. 2008, 2010); see also Lawson Handley et al. (2011) for a description of ABC methods. The DIYABC software allows probabilistic estimates of competing introduction scenarios, using prior historical, biological and genetic information

about the system to formally test hypotheses of invasion scenarios.

The data strongly suggest that the invasive populations in the east and west of North America originated from two independent introductions from the native range. The eastern North American population then acted as a bridgehead for the invasion, with separate introductions from this population into South America, Africa and Europe (though the European populations were admixed with individuals from biocontrol populations) (Lombaert et al. 2010). These invasion scenarios are supported with very high posterior probabilities (Lombaert et al. 2010). The findings also suggest that for *H. axyridis*, a still unknown evolutionary shift towards characteristics allowing invasion success occurred in eastern North America. Unfortunately, microsatellite data showed that there is very low genetic differentiation in the native Asian range, making inferences of the specific source population difficult. However, preliminary results from mitochondrial DNA (mtDNA) (Thomas et al. 2010) suggest greater population structure in the native range, which should help to pinpoint source populations more specifically.

In addition to the mtDNA analyses, further work is ongoing to address: (i) the genetic relationships between European biocontrol strains of *H. axyridis*; (ii) the genetic structure of *H. axyridis* within its native range and potential effects of such structure on inferences about invasion routes; (iii) the detailed genetic structure within each introduced area, to investigate the number of founders of invasive populations and the likelihood of multiple introduction events; (iv) the possibility that distribution of bacterial endosymbionts could shed additional light on invasion routes. Progress so far is outlined below:

- (i) In agreement with historical information, the common genetic origins of all the European strains used for biocontrol in Europe and South America were confirmed using microsatellite data, i.e. they are all derived from a single population of *H. axyridis* sampled from the native area by Institut National de la Recherche Agronomique (INRA) in 1982 (E. Lombaert and A. Estoup, unpublished data).
- (ii) The microsatellite and mtDNA data suggest that the genetic structure of *H. axyridis* within its

native Asian range consists of two groups: one located in the east of the range and one located in the west. Historical information about biocontrol practices (Tedders and Schaefer 1994; Krafur et al. 1997), and current airline transportation networks (e.g. Tatem and Hay 2007), suggest eastern Asia is the more likely source of the American outbreaks, which is why only *H. axyridis* populations from eastern Asia were considered as potential source populations in Lombaert et al. (2010). Interestingly, new DIYABC analyses of microsatellite data, taking into account the above genetic structure within the native range, indicated that populations from western Asia also contributed in a significant manner to the invasive bridgehead population located in eastern North America (E. Lombaert and A. Estoup, unpublished data) and indeed Gordon (1985) lists the Former USSR as a source of introduced *H. axyridis* biocontrol stock to eastern North America. For other invaded areas, the inferred invasion scenarios remained the same as those described in Lombaert et al. (2010), without significant contribution of populations from western Asia. If confirmed, this new finding may alter our understanding of key factors that could have enhanced the invasion potential of this ladybird. Indeed, after decades of unsuccessful acclimatization of biocontrol strains in North America, it is possible that admixture in eastern North America between genetically differentiated populations from the native range may have facilitated adaptation, by allowing the appearance of new genomic combinations. However, additional studies are needed in order to confirm this admixture event (e.g. using mtDNA, which shows greater differentiation in the native range) and assess the role of admixture in the success of this particular invasive bridgehead population (e.g. using quantitative genetics approaches).

- (iii) A detailed study of genetic structure at microsatellite loci within different introduced areas confirms the genetic homogeneity of invasive populations within each area, except Europe, and to a lesser extent, South America. For example, the populations sampled all over Europe clustered in several genetically differentiated groups, with one major group located in western Europe.

This group includes the invasive population from Ghent, Belgium analysed in Lombaert et al. (2010). Such preliminary results may indicate multiple introductions in Europe. Additional studies based on DIYABC analyses are needed in order to reconstruct the historical genetic relationships between these European populations, as well as between them and other invasive and native populations. Further data collection of mtDNA, to include additional populations from across each invasive continent, is ongoing. The complete dataset will be analysed in DIYABC, and by more traditional methods, to address whether high genetic diversity is related to multiple introductions within invasive populations, and to investigate the numbers of maternal founders of invasive populations.

- (iv) Several bacterial endosymbionts have been identified in global populations of *H. axyridis* (Aebi and Zindel 2010; L. Lawson Handley and C. Thomas, personal observation). Since endosymbionts are typically transmitted vertically (from mother to offspring), their distributions could potentially shed additional light on invasion routes. This, together with the transmission dynamics of endosymbionts in *H. axyridis*, and their impact on host mitochondrial genomes, is currently under investigation.

Dispersal of *H. axyridis*

Dispersal is critical to the establishment and persistence of invasive populations, and understanding dispersal mechanisms is essential for predicting the spread of invasive species. However, dispersal can be complex and difficult to measure, particularly in highly mobile insects that are difficult to study using traditional mark-release-recapture experiments. Determining the probability of long-distance dispersal (LDD) by wind or anthropogenic means is particularly important for predicting spread of an invasive species, as this can accelerate the rate of range expansion (Urban et al. 2008; Lawson Handley et al. 2011). However, short-distance dispersal (SDD) is important for local population dynamics, hence both SDD and LDD should be considered in predictive models. Indeed, a combination of SDD and LDD

(i.e. “stratified dispersal”) may be a common feature of invasions, and has already been described in several invasive insects, e.g. *Phyllonorycter leucographella* (Zeller) (Lepidoptera: Gracillariidae) (Nash et al. 1995), *Lymantria dispar* L. (Lepidoptera: Lymantriidae) (Sharov and Liebhold 1998), *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae) (Gilbert et al. 2003), *Cameraria ohridella* Deschka and Dimič (Lepidoptera: Gracillariidae) (Gilbert et al. 2004) and see Lawson Handley et al. (2011) for a review. This is likely to be the case in *H. axyridis*, which is an active flyer and disperses locally in response to prey density to and from overwintering sites, but is also capable of passive LDD by both wind and anthropogenic means (see below). In order to fully understand the dispersal capability of species such as *H. axyridis*, we consider below: (i) the mechanism(s) of dispersal; (ii) the reasons for dispersal; (iii) the influence of abiotic factors such as geography or climate on dispersal, and; (iv) the role of anthropogenic dispersal.

Mechanisms of dispersal

Short-distance dispersal (SDD)

Ladybirds are generally active fliers, and flight is considered to be the most important process determining distribution (Van der Werf et al. 2000). Most studies of dispersal have however focused on walking rather than flight, and therefore underestimate the true dispersal ability. *Harmonia axyridis* is often considered to be “a good flyer” (e.g. Obata 1986; Hodek et al. 1993; Tourniaire et al. 2000) with high dispersal capacity (Nalepa et al. 1996; Osawa 2000; With et al. 2002; Berkvens et al. 2009), and to be able to actively disperse over long distances to overwintering sites (Hodek and Honek 1996; Nalepa et al. 1996; Osawa 2000; With et al. 2002), but field and experimental data is scant. In field trials in Japan, control strains of *H. axyridis* had a median flight distance of 431 m for males and 396 m for females (Seko et al. 2008). In another field experiment, however, mean distance travelled by individuals (in a 3.3–7.6 day period) was considerably lower (9.71 ± 1.29 m), with females moving further than males in this case, and males moving slightly further in spring than in summer (Osawa 2000). This illustrates the difficulty of assessing dispersal distance in the field. It is also

difficult to evaluate the dispersal ability of *H. axyridis* without comparative data from other coccinellids, and flight experiments are needed in order to test this. A mark-recapture study of native coccinellids in Great Britain reported a maximum dispersal distance of 1.5 km (Zhou et al. 1994). So far, the only experimental data on *H. axyridis* flight ability comes from comparisons of selected flightless strains and non-selected laboratory strains (Tourniaire et al. 2000; Seko et al. 2008), which are unlikely to be representative of natural populations.

Long-distance dispersal (LDD)

An estimated spread rate of 442 km year^{-1} by *H. axyridis* in North America was calculated by McCorquodale (1998). Taking Europe as a whole, we have calculated that *H. axyridis* has spread at a maximum rate of approximately 200 km year^{-1} . This calculation is based on a south-easterly spread from Belgium, the Netherlands or northern France to Bulgaria (approximately 1600 km) in an eight year period. More detailed calculations for Great Britain reveal a northerly spread rate of 105 km year^{-1} (data from 2004 to 2008) and a rather faster westerly spread rate of 145 km year^{-1} . In South Africa, the species spread at a rate of approximately 500 km year^{-1} (Stals 2010). The European and North American calculations include the effects of multiple intentional biological control releases of *H. axyridis*. Whilst this does not apply to the British and South African calculations (where the species is not known to have been deliberately introduced), the dispersal rates in all regions were influenced by further anthropogenic factors (such as inadvertent dispersal with produce) which presumably played an important, but unquantifiable, part. The American figures were used to estimate a likely dispersal of >10 km per release for $>25\%$ of released beetles, giving an Environmental Risk Index (ERI) of 80 for *H. axyridis*. This is above the recommended threshold, indicating that the species should not be intentionally released (van Lenteren et al. 2008). Although these calculations are unquestionably useful, they were obtained indirectly from historical data which may be incomplete, and more direct, quantitative estimates of dispersal are needed. As yet, the mechanisms driving this spread, and the comparative roles of active flight, passive wind dispersal, and

anthropogenic spread are poorly understood (Hodek et al. 1993).

Reasons for dispersal

It is generally accepted that coccinellids perform four main types of active dispersal, classified according to the motivations behind them: 1. trivial appetitive flight (i.e. short-distance flight, e.g. to find prey); 2. hectic appetitive flight (i.e. long-distance flight initiated by overpopulation and the resultant prey shortage); 3. migration to overwintering sites and; 4. non directional dispersal from overwintering sites (Hodek et al. 1993). Non directional dispersal refers to that which is either passive (e.g. wind-induced) or somewhat random in nature.

Coccinellid flights of less than 2 m undoubtedly correspond to trivial appetitive flight (Elliott et al. 2000), but the cut off distance between trivial and hectic appetitive flight is difficult to quantify. Osawa (2000) inferred a mean dispersal distance of *H. axyridis* of 9.7 m (obtained from April to July) that likely includes both trivial and hectic appetitive flight. Aphids are arguably the biggest ecological predictor of dispersal in coccinellids such as *H. axyridis*. Appetitive flight is associated with foraging and ovipositioning behaviour, and is linked intricately with aphid population dynamics. This type of dispersal is essential in *H. axyridis* and other aphidophagous coccinellids, due to the ephemeral nature of their prey. Density of adult ladybirds is often positively correlated with aphid density (e.g. Turchin and Kareiva 1989; Hodek and Honek 1996; Osawa 2000; Evans and Toler 2007), and there is strong evidence that emigration rate decreases with increasing number of prey (see Evans (2003) for a review). Short-distance prey searching has been studied in many coccinellids (Banks 1956; Carter and Dixon 1982; Nakamuta 1982, 1984, 1985; Osawa 2000), and *H. axyridis* is highly effective at resource tracking, which enables it to maintain stable populations in temporally and spatially heterogeneous habitats and in pursuit of its prey (Osawa 2000). Therefore SDD is possibly determined by patterns of resource distribution within a habitat (Osawa 2000). Although some authors have suggested that visual and olfactory cues are important in coccinellids migrating to a particular habitat (e.g. Carter and Dixon 1982; Obata 1986; van der Werf et al. 2000),

others have inferred that specific signals, such as honeydew odour, are not reliable cues for SDD (Osawa 2000). Trivial appetitive flight is also important for coccinellid reproduction. Since larvae are limited in their dispersal ability, parents must locate developing aphid colonies before oviposition and optimise timing with prey availability. Such flight is non directional (Hodek and Honek 1996). Dispersal is also an important mechanism for avoiding inbreeding, and could explain why inbreeding is low in wild coccinellid populations, e.g. *Adalia bipunctata* (L.) (Hurst et al. 1996).

While active dispersal for foraging and mate finding will usually occur at small spatial scales (within the same habitat), dispersal towards overwintering sites can occur at larger scales if suitable shelter is not available locally (Hodek et al. 1993; Grez et al. 2005). *Harmonia axyridis* is, however, commonly associated with urban areas, and sheltered sites such as man-made structures can often be found close to their foraging and ovipositioning locations. Thus some overwintering dispersal takes place at small spatial scales. Dispersal from overwintering sites is thought to consist of a series of short, exploratory flights in search of aphids.

Finally, hectic appetitive flight is an extension of trivial appetitive flight, performed at times of low food abundance. It is during these longer-distance dispersal events that coccinellids are carried to high altitudes on thermal currents and then passively transported via wind (Hodek et al. 1993). Occasionally, this can result in large groups of coccinellids being simultaneously deposited in the same location, and can explain huge aggregations (millions of beetles) such as those of *Coccinella septempunctata* L. seen in Great Britain in the summers of 1976 and 2009.

The influence of abiotic factors on dispersal

Even when aphids are abundant in a given habitat, a significant proportion of coccinellid adults disperse every day (Krivan 2008). There must therefore be other factors that are important in driving coccinellid dispersal. Effects such as habitat fragmentation are likely to strongly influence active dispersal across a landscape. Habitat fragmentation has been shown to affect dispersal in *Eriopis connexa* Mulsant (Grez et al. 2005) and *C. septempunctata* (Kareiva 1987).

It has been argued that temperature is the single most important predictor of insect flight (Taylor 1963). In *H. axyridis*, temperature acts as a cue for dispersal, with movement from overwintering sites commencing on the first day over 18°C after a period of colder weather (Heulsman et al. 2002). There are upper and lower temperature thresholds between which take-off can occur, and between which aerial densities (and hence dispersal) are maximal (Taylor 1963). The wider the thresholds, the greater is the probability that an alien species will adapt to a wide range of climatic conditions. Given the climatic conditions encountered in the native range, from tropical southern Japan to Siberia, it is likely that *H. axyridis* has a very broad temperature threshold. There is likely to be considerable local adaptation to regional climate regimes across the geographic range. Nevertheless, it may be that the heterogeneous nature of its native range has equipped *H. axyridis* with valuable flight adaptations which have helped in its colonisation of a wide range of novel environments.

Wind is also important in insect dispersal and generally increases with altitude, with wind speeds being either facilitative or inhibitory, depending on their magnitude. The “flight boundary layer” (FBL), a term coined by Taylor (1974), is the theoretical altitude at which the wind speed exceeds the maximum flight speed of an insect. For directional SDD (e.g. for foraging), insects must remain below their FBL so that they are free to perform active flight. By contrast, LDD for colonisation is facilitated by high wind speeds above the FBL. Although the height of the FBL is unknown for *H. axyridis*, there is evidence from Vertical Looking Radar (VLR) (Riley and Reynolds 1997; Chapman et al. 2003) of large coccinellids flying at high altitudes (D. Jeffries, unpublished observation). This suggests that LDD of *H. axyridis* could be facilitated by passive transport at high altitudes. Indeed, since the first observations of *H. axyridis* in Great Britain were concentrated in the south-east, one plausible route of entry to Britain is via passive dispersal on winds across the English Channel (Brown et al. 2008b). However, it is unlikely that passive wind dispersal alone can explain the spread of *H. axyridis* in Britain, since observational records strongly indicate a north-westerly spread (Brown et al. 2008b) in contrast to the prevailing south-westerly wind. The spread of *H. axyridis*, at least in Britain, presumably therefore involved a considerable component of active flight.

Determining what constitutes a barrier to dispersal is essential for predictive modelling of the spread of invasive species. Both temperature and wind are likely to be important, since lower temperatures may inhibit dispersal and higher wind speeds mean less control over directed flight. These conditions are affected by landscape topography, so it seems fair to assume that mountain ranges may act as dispersal barriers, even for active-flying insects. Whilst this could explain why the main British distribution of *H. axyridis* is bordered by the Pennine and Cambrian Mountains, the role of mountain ranges as dispersal barriers warrants formal investigation.

The role of anthropogenic dispersal

Anthropogenic dispersal has been an important factor in the spread of alien coccinellids (Evans et al. 2011). In the case of *H. axyridis*, anthropogenic dispersal has taken various forms, both deliberate (i.e. use in biological control) and inadvertent, and there is no doubt that collectively these have been key to the very rapid spread of the species. Transport of *H. axyridis* with produce such as fruit, vegetables and flowers was documented, with clear examples of range expansion evident, e.g. first records from Norway (Staverloekk et al. 2007), northern England (Brown et al. 2008b), Northern Ireland (Murchie et al. 2008) and Orkney, northern Scotland (Ribbands et al. 2009). Inadvertent dispersal with people in motor vehicles and trains is a further mechanism. For example, the first record of *H. axyridis* in Scotland arose from the beetle being transported in a suitcase (Holroyd et al. 2008). Intercontinental anthropogenic dispersal of *H. axyridis* has also been observed. For example, over 2000 adult *H. axyridis* were accidentally transported on timber from the USA to Norway (Saethre et al. 2010), and the species was found in Great Britain on packing cases from Canada (Majerus et al. 2006). Further examples of the potential for large numbers of a coccinellid to be transported anthropogenically were provided by Minchin (2010) and Brown et al. (2011b), who each reported several thousand *C. septempunctata* being transported on ships, from South America to northern Africa in the former case and from Denmark to England in the latter. *Harmonia axyridis* has reached Australia by anthropogenic means at least twice (once from the USA and once from an unknown source country),

although in each case the beetles were either dead or intercepted during quarantine inspection (Smith 2008; Carvan 2009). Whilst these examples do not all provide subsequent evidence of establishment of the alien species in the new region (which is dependent on many factors, including the number of beetles transported and climatic and habitat suitability in the new area), they clearly illustrate that accidental anthropogenic transport can be an important mechanism for the spread of invasive alien species such as *H. axyridis*. Nedvěd et al. (2011) outlined similar mechanisms involved in the spread of arachnids in Europe and North America. Some of the examples also indicate that *H. axyridis* is a species that is robust enough to survive very long journeys, and that its aggregative behaviour at certain times of the year is potentially an important feature in terms of dispersal.

Avenues for future research on dispersal

We are a long way from fully understanding the mechanisms and reasons for dispersal in *H. axyridis*, but technological developments could provide valuable insights. Physiological flight ability can be tested in flight mills (Hocking 1953), a method recently incorporated in assessments of *H. axyridis* residence periods in open fields (Seko et al. 2008). Harmonic radar, using diode transponders and tagged insects, can be used to study insect activity at ground level (Riley and Smith 2002). This technique has provided unique insights into the foraging behaviour of the honeybee *Apis mellifera* L. (Hymenoptera: Apidae) (Capaldi et al. 2000), and the dispersal of the Glanville fritillary *Melitaea cinxia* (L.) (Lepidoptera: Nymphalidae) (Niitepold et al. 2009), and could be particularly useful for studying SDD in *H. axyridis* and other coccinellids. VLR technology provides an opportunity to study long-distance wind-borne dispersal, vertical distribution and insect layering, and temporal variation in dispersal (Chapman et al. 2002, 2003, 2010). One VLR study showed that a large migration from the Netherlands of the diamondback moth *Plutella xylostella* (L.) (Lepidoptera: Yponomeutidae) occurred in May 2000, and that this migration route was responsible for the re-establishment of the species in Great Britain (Chapman et al. 2002). Recent studies have used meteorological and VLR data to backtrack dispersal trajectories of noctuid

moths, showing that they can compensate for cross-wind-drift to maximise their long-distance migration efficiency (Chapman et al. 2010). Similar techniques could be used to investigate the dispersal and spread of *H. axyridis*, and provide a more concrete answer to the question of whether regular dispersal occurs, e.g. from the European mainland to Great Britain. Aside from radar technologies, genetic studies are already providing insights into the global spread of *H. axyridis* (Lombaert et al. 2010 and see above), and a landscape genetics approach is currently being used to indirectly investigate dispersal barriers in the native range (Lawson Handley et al. 2011). Additional studies could provide insights into the genes underlying dispersal, and in combination with harmonic radar, be used to investigate the relationship between dispersal, genotype, physiology and environment, as recently demonstrated in *M. cinxia* (Niitepold et al. 2009).

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