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Harmonia axyridis in Europe: spread and distribution of a non-native coccinellid

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Abstract Native to Asia, Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae) is considered an invasive alien ladybird in Europe and North America, where it was widely introduced as a biological control agent of aphids and coccids. In Europe, *H. axyridis* was sold by various biological control companies from 1995 in France, Belgium and the Netherlands, and was also intentionally released in at least nine other countries. It has spread very rapidly, particularly since 2002, and is now regarded as established in thirteen European countries. The established range extends from Denmark in the north to southern

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France in the south, and from Czech Republic in the east to Great Britain in the west. In this paper we map the spread and distribution of *H. axyridis* in Europe, and examine the situation on a country-by-country basis. We report first records of the species in five countries; Spain, Sweden, Denmark, Czech Republic and Italy; and first evidence of *H. axyridis* establishment in the latter three countries. Despite releases of *H. axyridis* in Portugal, Spain and Greece, there is little evidence of establishment in southern Europe. It is predicted that the spread and increase within Europe will continue and that *H. axyridis* will become one of the most widely distributed coccinellids in the continent.

Keywords Biological control · Coccinellidae · Halloween beetle · Harlequin ladybird · *Harmonia axyridis* · Introduced species · Invasive species · Multicolored Asian lady beetle · Non-native species

Background to *Harmonia axyridis*

Variously known as the multicolored Asian lady beetle, Halloween beetle and harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), is native to China, Japan, Korea, Mongolia and Siberia (e.g. Dobzhansky 1933; Kuznetsov 1997), although its entire native range, particularly in parts of the former Soviet Union, has not been clearly recorded. Although usually stated in the literature to be semi-arboreal (e.g. Hodek 1973), 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. submitted to BioControl SI), reedbeds (Ware et al. 2005; Brown et al. submitted to BioControl SI) and crop systems (Colunga-Garcia and Gage 1998).

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The species has a long history of use as a classical biological control agent of aphids and coccids in North America, where it was first introduced in 1916 (Gordon 1985). It has been widely used for pest control in crops as diverse as pecans (Tedders 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). Despite releases in fourteen US states between 1964 and 1982 (Gordon 1985), *H. axyridis* was not reported as established in the country until 1988 (Chapin and Brou 1991). There is uncertainty over the source of the established US population, which may originate from a single intentional release or accidental introduction (Krafsur et al. 1997). Day et al. (1994) suggested that the source could have been accidental seaport introductions.

Harmonia axyridis has recently been recorded in South America (de Almeida and da Silva 2002) and South Africa (N. Mgocheki, personal communication; J. Hatting, personal communication), and has been introduced in Egypt (Ferran et al. 2000) where it has become established around Cairo (S. Elnagdy, personal communication).

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). Various companies subsequently made the species commercially available (Adriaens et al. 2003).

In a risk assessment of 31 exotic natural enemies of pest species used in biological control in Europe, *H. axyridis* had the second highest environmental risk index. This was based on its wide host range (i.e. multiple prey species), ability to establish and disperse, and direct and indirect effects on non-target species (van Lenteren et al. 2003). Van Lenteren et al. (submitted to BioControl SI) concluded that there are no easy ways to mitigate or reduce the risk of *H. axyridis* and that it should not have been released in northwest Europe.

The aim of this paper is to present a thorough examination of the history, spread and distribution of *H. axyridis* in Europe. The data are an amalgamation of records of the occurrence of *H. axyridis* in Europe, mapped at 50 km resolution. Records were verified by the authors, derived from published papers, and/or made by experienced naturalists.

Countries in which *H. axyridis* was introduced as a biological control agent

Belgium

Harmonia axyridis was used as a biological control agent in Belgium from 1997 (Adriaens et al. 2003). A large-scale ladybird field survey (Coccinula—Belgian ladybird working group, http://www.inbo.be/content/page.asp?pid=EN_FAU_INS_LAD_start) was launched in 1999 in the Walloon region, and 2001 in the Flemish region (Adriaens et al. 2003). By 2007 Coccinula had in excess of 500 volunteer surveyors (Adriaens et al. submitted to BioControl SI), hence coccinellids are very well recorded in Belgium. *Harmonia axyridis* was first found in the wild in Belgium in autumn 2001, in both Ghent and Brussels (Adriaens et al. submitted to BioControl SI) and the invasion probably originated from populations in the north of the country. By 2003, *H. axyridis* was found in large overwintering aggregations comprising 500+ individuals (Adriaens et al. submitted to BioControl SI) and was invading semi-natural ecosystems (Adriaens et al. 2003). *Harmonia axyridis* was recorded most commonly in gardens and parks, road verges, forests

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and woodland fringes, but it also occurred in other habitats such as heathlands, meadows and wetlands (Adriaens et al. submitted to BioControl SI). By 2006, *H. axyridis* was recorded in all regions of Belgium (Fig. 1). The Coccinula database (data from 1999 to 2007) shows that *H. axyridis* was the most abundant coccinellid in Flanders, in terms of the total number of individuals recorded (excluding overwintering groups, which would have made *H. axyridis* abundance even higher). *Harmonia axyridis* was recorded in 76% (426 of 560) of sampled 5 km ^{2} in Flanders, making it the second highest occurring coccinellid after *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). In Belgium as a whole, *H. axyridis* was recorded in 49% (557 of 1139) of sampled 5 km ^{2}, making its occurrence fifth highest after *C. septempunctata, Propylea quatuordecimpunctata* (L.) (Coleoptera: Coccinellidae), *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) and *Thea vigintiduopunctata* L. (Coleoptera: Coccinellidae). A full account of the spread of *H. axyridis* in Belgium is provided by Adriaens et al. (submitted to BioControl SI).

Czech Republic

The flightless strain of *H. axyridis* was introduced into hop gardens in northwestern Czech Republic in 2003, but the species did not apparently establish at that time. The easterly

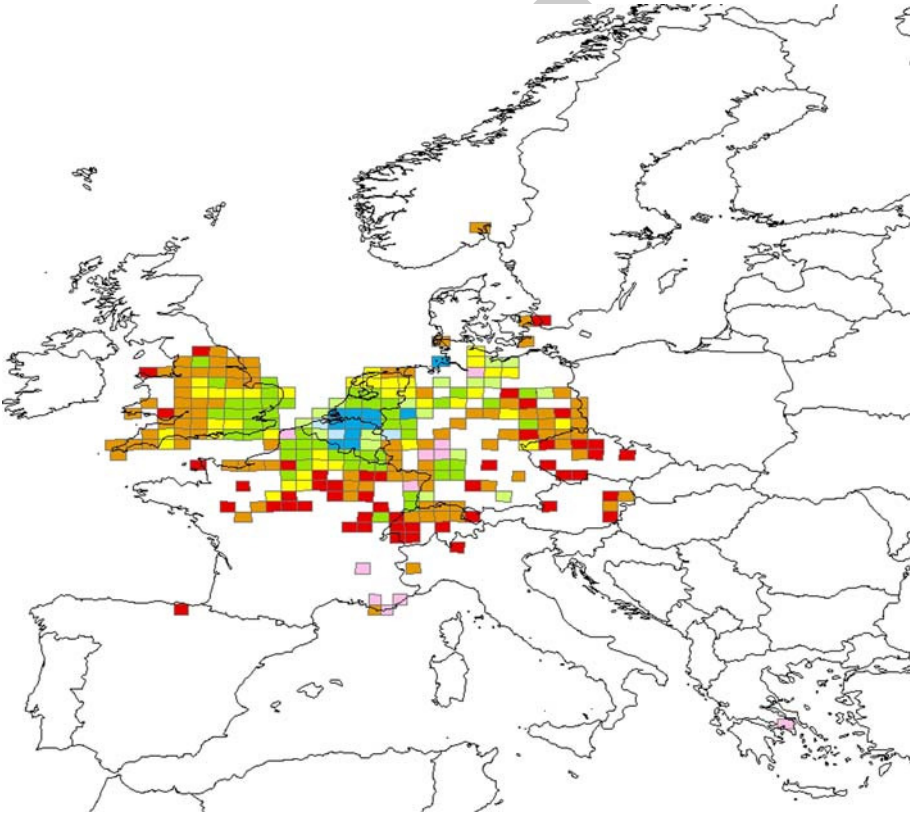

Fig. 1 Recorded occurrence of *H. axyridis* in 50 km ^{2} in Europe. (Year of first known record: red = 2007; orange = 2006; yellow = 2005; dark green = 2004; pale green = 2003; dark blue = 2002; pale blue = 2001; pink = pre 2001)

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spread of *H. axyridis* from Germany is assumed to be the main cause of the species arriving in the Czech Republic, where it was first recorded in the wild in 2006 in Prague and nearby rural areas (O. Nedved and I. Kovář, unpublished data). In 2007, intentional monitoring was started (advertised at http://zoo.bf.jcu.cz/kz/harmonia.htm), resulting in records from all parts of Bohemia and northern Moravia, the eastern-most recorded locality of *H. axyridis* in Europe (Fig. 1). Records of ovipositing females and mature larvae confirmed that the species had established. Most *H. axyridis* were found on aphid infested woody plants: cherry *Prunus avium* L. (Rosaceae), mock-orange *Philadelphus coronarius* L. (Hydrangeaceae), steeple-bush *Spiraea douglasii* Hook (Rosaceae), willow *Salix alba* L. (Salicaceae), crab apple *Malus sylvestris* (L.) Mill. (Rosaceae) and pear *Pyrus communis* L. (Rosaceae). Based on the findings of mature larvae and ovipositing females, five prey species; *Aphis philadelphi* Börner (Hemiptera: Aphididae), *Aphis spiraecola* Patch (Hemiptera: Aphididae), *Dysaphis plantaginea* (Passerini) (Hemiptera: Aphididae), *Tuberolachnus salignus* (Gmelin) (Hemiptera: Aphididae) and *Cacopsylla pyri* (L.) (Hempitera: Psyllidae); may be considered as suitable (essential sensu Hodek 1973) prey for *H. axyridis*.

France

Harmonia axyridis was first introduced to France from China by the Institut National de la Recherche Agronomique (INRA) (http://www.inra.fr) in 1982 (Iperti and Bertand 2001), but was in quarantine until 1990 (Kabiri 2006). Between 1990 and 1997 field experiments and releases were carried out, especially in southeastern France, but also in the north of the country and near Paris (Coutanceau 2006). Mass production of *H. axyridis* in France began in 1992 and the first open-air commercial field releases were in 1995 (Kabiri 2006). The species is regarded by Coutanceau (2006) to have become acclimatized in France by 1991. The earliest known record in the wild is of two individuals, both of the colour form f. *spectabilis* (Fig. 2), found at Saint-Aubin (Lot-et-Garonne) in southwestern France in November 1991 (Coutanceau 2006). *Harmonia axyridis* was recorded at five overwintering sites in southern France between 1992 and 1993 (Coutanceau 2006) and at Pas-de-Calais in northern France, where it was released in hops in 1994 (Trouvé 1995). There are very few known records of *H. axyridis* in France from 1995 to 2003, but from 2004 it was widely established (Coutanceau 2006) and by 2007 was found across much of northern France (Fig. 1). It is unknown whether the sparseness of records prior to 2004 is a result of lack of recording effort, or genuine scarcity of *H. axyridis* in France at that time. Certainly, since 2004 the recording effort in France has increased, principally due to the launch of a dedicated survey (Observatoire *H. axyridis*–http://perso.orange.fr/vinc.ternois/cote_nature/Harmonia_axyridis). This is now a well organised survey with in excess of 120 contributors in 15 French regions, each having a regional co-ordinator.

Germany

Although officially never sold in Germany, *H. axyridis* was released in Frankfurt between 1997 and 1998 to control aphids on roses (H. Bathon, unpublished data). It was first recorded in the wild in 1999 in Hamburg (Tolasch 2002) and Frankfurt-Niederrad (H. Bathon, unpublished data). By 2000, *H. axyridis* was common in the Rhein-Main region and there was major expansion of the species in Germany by 2002 (Klausnitzer 2002).

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Fig. 2 *H. axyridis* f. *succinea*, f. *spectabilis* and f. *conspicua.* (**a**) © Gavin Hatt, John Innes Centre Entomology, (**b**) © Ken Dolbear, (**c**) © Gavin Hatt, John Innes Centre Entomology

By 2006, *H. axyridis* occurred in all regions of western Germany and was common in many cities (F. Köhler, personal communication). The species is well recorded in central eastern Germany from 2006, but there are few records from the northeast or southeast of the country (Fig. 1). This may be due to lower recording effort rather than genuine absence of the species.

Greece

French stock of *H. axyridis* was introduced into four citrus-growing areas of Greece in 1994 (Katsoyannos et al. 1997). From 1995 to 1999 over 100,000 adult *H. axyridis* were released in central and southern Greece and on several islands, to control aphids on various crops (including citrus, vegetables, beans and maize) (Kontodimas et al. in press). Further releases took place from 1997 to 2002, mainly in urban areas (Attica and Peloponessos regions, Corfu, Rhodes and Crete) (Kontodimas et al. in press). Despite these major releases and four overlapping generations of *H. axyridis* being reported in Greece (Katsoyannos et al. 1997), there is little evidence of establishment of the species, although small numbers (<50) of overwintered adults were found in Attica in spring 1998 and 1999 (Kontodimas et al. in press) (Fig. 1).

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Italy

Harmonia axyridis was used as a biological control agent in greenhouses in northern Italy in the 1990s. The first known sighting of *H. axyridis* naturalised in Italy, was in Turin in October 2006, when approximately 30 specimens, including pupae, were found on trees of an *Acer* sp. (Aceraceae) (I. Zakharov, unpublished data) (Fig. 1). It is unknown whether these ladybirds originated from escaped specimens within Italy, or are immigrants from southern France or Switzerland. In July 2007, a few adult *H. axyridis* were found at two sites in the Piedmont region (M. Kenis, unpublished data), presenting further evidence of establishment in northeastern Italy.

Netherlands

Harmonia axyridis was marketed as a biological control insect in the Netherlands from approximately 1996 (Cuppen et al. 2004) until 2003. The first record of *H. axyridis* naturalised in the Netherlands was in October 2002, when a pupa was found on an ivy *Hedera helix* L. (Araliaceae) leaf in Nijmegen. A larva of *H. axyridis* was confirmed in Rotterdam the following month. Initial distribution was reported primarily in the southern half of the country. Numbers of *H. axyridis* rose dramatically from 2004 (Loomans 2004) and survey effort was increased from that year, with records requested via three Dutch websites (http://www.stippen.nl, http://www.knnv.nl and http://www.nev.nl). The species appears to have spread from south to north, and by 2006 all mainland 50 km ^{2} in the Netherlands had records of *H. axyridis* (Fig. 1). Over 2000 records of the species were received between 2002 and 2007.

Portugal

Between 1984 and 1985, *H. axyridis* was used to control aphids on citrus crops in the Algarve province of Portugal, and on the Portuguese administered islands of the Azores (Katsoyannos et al. 1997; Soares et al. submitted to BioControl SI). There is no evidence of subsequent establishment. However, recent work by Soares and Serpa (2007) concluded that if re-introduced to the Azores, *H. axyridis* would present a risk to the native species *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae).

Spain

In 1995 *H. axyridis* was introduced to control aphids on greenhouses in Almeria, southeastern Spain (SIFA 2004). It established in greenhouses (Jacas et al. 2006), but there is no evidence of subsequent establishment in the wild. In 2003 and 2004 two specimens of *H. axyridis* were found in a garden on Tenerife, Canary Islands and it was found again on the island in 2006 (S. Eizaguirre, personal communication). There are no official reports of introductions of *H. axyridis* for agricultural purposes from the Canary government, and the species is not believed to be present in large numbers (Machado 2005). In 2007, two adult *H. axyridis* were collected from flowers of a *Tilia platyphyllos* Scop. (Tiliaceae) tree in a park in Loiu, Bilbao, Basque country of northern Spain (A. Goldarazena, unpublished data) (Fig. 1). This is the first record of naturalised

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H. axyridis in the Iberian peninsula. There is no evidence that *H. axyridis* was released for biological control purposes in the Basque country (R. Amenabar, personal communication). The specimens are likely to have either originated from France, or from imported goods entering the nearby Bilbao airport.

Switzerland

Harmonia axyridis was available commercially in Switzerland for a short period in the late 1990s, and was used in a small field trial on roses in Grossdietwil in 1996 (Andermatt 1996). However, *H. axyridis* did not apparently establish as a result, and applications for the commercial release of the species were refused by the Swiss Pesticide Regulatory Authority in 1997 (van Lenteren et al. submitted to BioControl SI). No adults were found in the wild in Switzerland until 2004, when a single specimen was found at an exhibition of Asian plants in Basle (Klausnitzer 2004). *Harmonia axyridis* was not found during surveys in 2005, but in 2006 it was recorded in ten cantons in northern Switzerland (Eschen et al. 2007), and larvae of the species were found for the first time in Switzerland. The higher abundance of the beetle near the northern border suggests that it invaded the country from southern Germany and/or eastern France. In a large survey for ladybirds in northwestern Switzerland, *H. axyridis* was found to be the seventh most abundant species on trees and shrubs, and the first cases of aggregations on buildings were notified in autumn 2006 in Basle, where the species was the most abundant coccinellid at some sites (Eschen et al. 2007). The monitoring continued in 2007 and a dedicated website was launched (http://www.cabi-bioscience.ch/harmonia). By late 2007, the ladybird was found in most Swiss cantons (Fig. 1).

Countries in which *H. axyridis* has been found in the wild without evidence of deliberate introduction

Austria

In Europe and North America, the attraction of *H. axyridis* to buildings for use as overwintering sites (Koch 2003) has increased the number of sightings of the species. The first published record in Austria (October 2006; Wiener Neustadt, eastern Austria) was one such sighting, where several adult specimens of *H. axyridis* were found on a house wall searching for an overwintering site (Rabitsch and Schuh 2006). An earlier record subsequently came to light, in which *H. axyridis* larvae were found on plants on a balcony in nearby Vienna in July 2006, and there are several later records of adults in Vienna in 2006 and 2007 (W. Rabitsch, unpublished data). *Harmonia axyridis* is clearly established in Austria, and independent observations in the west (Götzis, October 2006; Rankweil, April 2007; Vorarlberg, August 2007), centre (Salzburg, May 2007), and south (Herberstein, July 2007) of the country (W. Rabitsch, unpublished data), support the hypothesis of spread from Switzerland and/or Germany (Fig. 1). There is no known evidence that *H. axyridis* was used for biological control purposes in Austria, making it less likely that the spread resulted from (illegally) imported specimens escaped from greenhouses or gardens. The scattered documentation of *H. axyridis* in Austria reflects the largely unnoticed expansion in the country. No large aggregations have yet been reported, with the maximum number from a single site (Vienna) being approximately 20 adult *H. axyridis*.

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Denmark

The first known record of *H. axyridis* in Denmark was in Copenhagen in July 2006 (J. Pedersen, unpublished data). Then and on five subsequent occasions in August 2006, October 2006 and June 2007, a total of 14 adults of *H. axyridis* were found in a light trap. Similarly, a single adult was found in a light trap at Mandemarke, in each of August 2006 and July 2007 (J. Pedersen, unpublished data) (Fig. 1). All specimens were f. *succinea* (Fig. 2). Denmark is the most northerly country in Europe where *H. axyridis* is thought to have established. It is not known to have been introduced there and is assumed to have spread north from Germany.

Great Britain and the Channel Islands

The first record of *H. axyridis* in Great Britain, in September 2004, initiated considerable media and public interest, and led to the launch of the web-based Harlequin Ladybird Survey (http://www.harlequin-survey.org) (Majerus et al. 2006; Roy et al. 2006). Thanks to thousands of contributors across Britain, the species has been recorded and mapped at high resolution (Roy et al. 2005; Brown et al. submitted to BioControl SI) and its rapid spread north and west from the southeast is clear (Fig. 1). By mid 2007, *H. axyridis* was recorded in 88% of English and 38% of Welsh vice counties. It was also found on the island of Jersey, Channel Islands. We predict that it will continue to spread north and reach Scotland by the end of 2008. Three colour forms have been recorded in Britain; f. *succinea*, f. *spectabilis* and f. *conspicua* (Fig. 2). A detailed account and analysis of the spread of *H. axyridis* in Great Britain is provided by Brown et al. (submitted to BioControl SI).

Liechtenstein

Harmonia axyridis was found for the first time in the tiny principality of Liechtenstein in August 2007 (A. Loomans, unpublished data). The whole principality is contained within a single 50 km^2 in which there were earlier records for both Austria and Switzerland.

Luxembourg

Considering that the border areas of France, Belgium and Germany that surround Luxembourg were all known to have populations of *H. axyridis* (Fig. 1), it was inevitable that the species would arrive in this small country. It was present by September 2004, when first recorded on *Acer pseudoplatanus* L. (Aceraceae) in the south of Luxembourg (Schneider and Loomans 2006). Further sightings of *H. axyridis* were made in October, November and December 2004 in urban locations (Schneider and Loomans 2006) and large reproducing populations were recorded in August 2005 in the north (Clervaux) and south (Luxembourg City) of the country (M. Majerus, unpublished data).

Norway

Whilst there is no evidence that *H. axyridis* is established in Norway, it has been recorded in Oslo, having been found on horticultural plants imported from the Netherlands in April 2006 (Staverloekk et al. in press) (Fig. 1).

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Sweden

Harmonia axyridis was first recorded in Sweden in Malmö in April 2007 (T. Hägg, unpublished data), when a single adult was found in a house (Fig. 1). Subsequently, a dead adult was found at the same location, and it is thought that the species had been overwintering in the house, suggesting that it arrived in late 2006, possibly from Germany or Denmark. There are no other known records of *H. axyridis* in Sweden.

Establishment and spread

Harmonia axyridis has spread in Europe at a very fast rate (Table 1; Fig. 3). It is not possible to fully explain the mechanisms of spread leading to the current distribution, because of the spatial and temporal aspects of the deliberate releases of *H. axyridis*. This involved multiple introduction sites in at least twelve European countries over a period of approximately forty years (Table 1).

Time lags may occur throughout the invasion process, including the arrival, establishment and impacts of the invading species (Crooks 2005). Our data indicates a variable time lag between initial establishment and major expansion, at least in the countries where *H. axyridis* was deliberately introduced. In France this time lag was approximately

Table 1 Summary of *H. axyridis* occurrence in Europe

Country	Year of first record in the wild	Deliberately introduced? (Earliest year of introduction)	Evidence of establishment?	No. 50 km^2 with *H. axyridis* by August 2007
Ukraine	Unknown	Yes (1964)	Unknown	Unknown
Belarus	Unknown	Yes (1968)	Unknown	Unknown
Portugal	N/A	Yes (1984)	No	0
France	1991	Yes (1982)	Yes	63
Greece	1998	Yes (1994)	Limited	1
Germany	1999	Yes (1997)	Yes	75
Belgium	2001	Yes (1997)	Yes	21
Netherlands	2002	Yes (1996)	Yes	26
Spain, including Canary Islands	2003	Yes (1995)	No	2
Switzerland	2004	Yes (1996)	Yes	15
Luxembourg	2004	No	Yes	2
England and Channel Islands	2004	No	Yes	60
Italy	2006	Yes (1990s)	Yes	1
Czech Republic	2006	Yes (2003)	Yes	11
Austria	2006	No	Yes	7
Denmark	2006	No	Yes	2
Wales	2006	No	Yes	5
Norway	2006	No	No	1
Liechtenstein	2007	No	Yes	1
Sweden	2007	No	No	1

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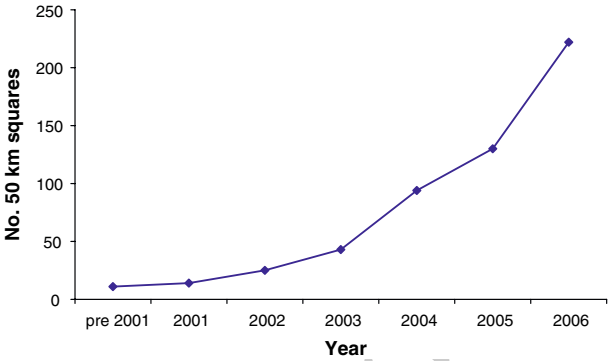

Fig. 3 Cumulative occurrence of *H. axyridis* in 50 km ^{2} in Europe

13 years (i.e. 1991–2004), in the Netherlands approximately 6 years (i.e. 1996–2002), and in Belgium approximately 4 years (i.e. 1997–2001). In countries where the species has not known to have been introduced, there seems to be very little time lag between the first record of establishment and major expansion (e.g. less than one year in England). The period between establishment and rapid spread in the USA is difficult to assess because of multiple intentional releases over many years (Gordon 1985), uncertainty over the date of establishment, and ambiguity over whether an intentional release or an accidental introduction was the source of establishment (Day et al. 1994; Koch 2003).

The reasons for the time lag between establishment of *H. axyridis* and major expansion in Europe are as yet unknown. However, it is possible that it is related to the genetic make-up of releases, and to differences between environmental conditions in the locations where released stocks originated and where they were released. The genetic make-up of released stocks would be a function of selection acting to locally adapt populations in their native range before collection, and random genetic drift and selection acting on laboratory cultures before release. It is likely that some cultures passed through genetic bottlenecks while in culture. Moreover, there are reports of rapid changes in some obvious genetically controlled traits in laboratory cultures. For example, the phenotypic frequencies of melanic forms (f. *conspicua* and f. *spectabilis*) of a laboratory population increased from 0.5 to >0.99 in 50 generations (Berkvens et al. submitted to BioControl SI). As many laboratory cultures are maintained on diets that *H. axyridis* would not encounter in the wild (i.e. *Ephestia* eggs), it is inevitable that released beetles will have been exposed to abnormal selection pressures in captivity. In consequence, it is highly unlikely that released individuals will be precisely adapted to the conditions that they face in their introduced range. In many cases, releases therefore do not lead to establishment, as recorded for *H. axyridis* in the USA (Gordon 1985) and Greece (Kontodimas et al. in press). However, if we assume that at least some individuals do survive and reproduce, the expectation would be that these would take time to start increasing in number significantly, for two reasons. First, because of their as yet imperfect adaptation to local conditions, and second because at low population size they are likely to suffer the effects of inbreeding depression, which is considerable in many aphidophagous coccinellids (Hodek 1973; Majerus 1994, 2003). There will thus be a period after establishment during which the average fitness of members of the population increase as the population is purged of deleterious recessives (Haldane 1927), and slowly becomes better locally adapted to the new conditions, through selection acting on the genotypic variation generated by recombination and mutation (Fisher 1930). It is only once the population has become locally adapted that it will start to

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increase in number. However, the rate of increase may then be rapid for two reasons. First, the population may have been purged of deleterious recessive alleles, as mentioned above. Second, while in culture the released beetles may have been inadvertently selected for rapid reproduction, high fecundity and broad dietary range; biological control companies reared large numbers as efficiently as possible for commercial reasons. Once numbers in a released population increased sufficiently to approach carrying capacity, increased rate of dispersal would be inevitable as the beetles sought new resources. The rate of this process may vary greatly depending on factors such as the size of the original samples collected from the native range, the number of different populations that such samples were collected from, the length of time and number of generations that cultures were kept in captivity for before release, the number of individuals that founded each culture generation, and the number of beetles finally released. If releases involved stocks with quite different origins, then the speed of local adaptation would be faster than if all released beetles were from a single stock. This is because matings between individuals from different locally adapted populations would produce a greater range of genetic variants among their offspring for selection to act upon.

The initial need for adaptation before increase in number and spread may explain the lack of a time lag between establishment and major expansion in countries where *H. axyridis* was not deliberately introduced; individuals of *H. axyridis* arriving in these countries from parts of the introduced range had already been through the adaptation phase. So after a period of adaptation of one or several populations in France, Netherlands, Belgium and/or Germany, a rapid spread of *H. axyridis* occurred throughout Europe.

Genetic variation and the origins of *H. axyridis* in Europe

Three main colour forms of adult *H. axyridis* have been found in Europe: f. *succinea*, f. *spectabilis* and f. *conspicua* (Fig. 2). The typical form *axyridis*, which predominates in central Asia (Dobzhansky 1933; I. Zakharov and M. Majerus, personal observation), has not yet been recorded in Europe. The *succinea* complex has been divided into many subforms (e.g. *siccoma*—0 spots; *frigida*—6 spots; *novemdecimsignata*—19 spots) (Dobzhansky 1933), but is regarded as a single form here. Thus f. *succinea* has elytra with a ground colour of yellow, orange, or red, and 0–21 black spots, which may or may not be fused. Forma *spectabilis* has black elytra with four yellow, orange, or red spots or other shaped markings, which sometimes contain a central black spot. Forma *conspicua* is as f. *spectabilis*, but with only the anterior pair of spots.

There is strong evidence of a link between climate and colour form in coccinellids (e.g. Majerus 1994, 1998). Whilst the basis of difference in distinct colour form (e.g. f. *succinea* cf. f. *spectabilis*) is genetic, difference in colouration within a form is at least partly environmental. For example, in many species of coccinellid, inverse correlations between temperature and extent of melanic patterning have been reported (e.g. Dobzhansky 1933; Abbas et al. 1988; Majerus 1998). In the case of *H. axyridis*, the amount of melanism in f. *succinea* was found to increase at high elevations (Nalepa et al. 1996).

European populations of *H. axyridis* generally include a mix of the three colour forms, but with f. *succinea* predominating (Fig. 4). Interestingly, in England the percentage of melanic specimens declined markedly from the year of arrival of *H. axyridis*, 2004 (45%, $n = 344$) (Majerus and Roy 2005) to the second year, 2005 (20%, $n = 6180$) (M. Majerus, unpublished data). The broad consistency in the colour form frequency data from Europe (Fig. 4) provides some evidence of the genetic similarity of populations in different

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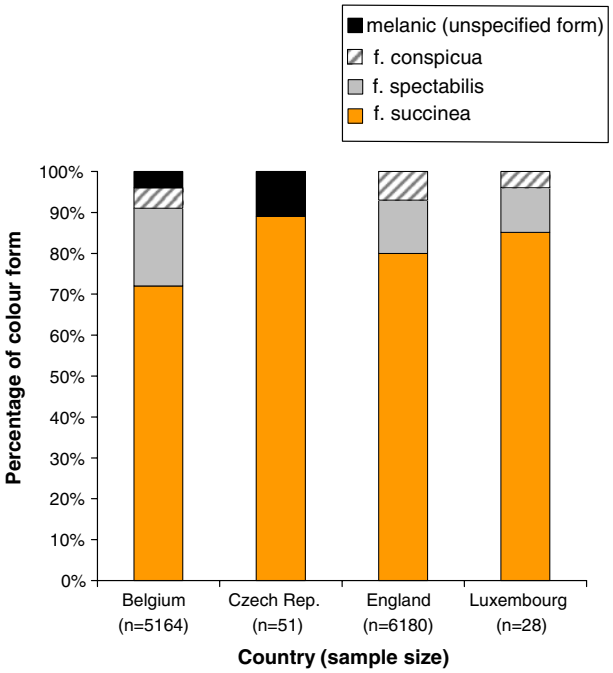

Fig. 4 Percentages of *H. axyridis* colour forms in various countries (Belgium data from 2004–2006 (Adriaens et al. submitted to Biocontrol SI), Czech Republic data from 2006–2007 (O. Nedved, unpublished data), England data from 2005 (M. Majerus, unpublished data), Luxembourg data from 2004 (Schneider and Loomans 2006))

European countries. Further, we suggest that this possible genetic similarity is the result of spread of the species from very limited points of origin in Europe. Genetic analyses of *H. axyridis* samples from different countries are needed in order to confirm this.

Traits that give *H. axyridis* a competitive advantage over native coccinellids

In Europe, *H. axyridis* has been shown to be multi-voltine, with evidence of four generations per year in Greece (Katsoyannos et al. 1997) and two generations per year in Great Britain (Brown et al. submitted to BioControl SI). Production of multiple generations would help to explain the rapid spread of *H. axyridis* in Europe. In northern Europe, many native coccinellids are uni-voltine (Majerus 1994; Klausnitzer and Klausnitzer 1997), thus *H. axyridis* may have a significant advantage over them in terms of potential population growth. Dispersal of *H. axyridis* in northern Europe appears to occur primarily in autumn, when the species moves to aggregate at overwintering sites. This pattern is similar to that observed in North America (Koch 2003). Large overwintering aggregations have been observed in several European countries including Belgium, the Netherlands, France, Germany and England.

Recent European research has provided further evidence of the adaptability and resilience of *H. axyridis*. In laboratory experiments, 35–48% of *H. axyridis* larvae fed a pollen-only diet successfully reached adulthood, and although fitness was reduced, approximately

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40% of these adult females produced viable eggs (Berkvens et al. submitted to BioControl SI). Roy et al. (submitted to BioControl SI) found that only the highest dose (10^9 spores ml^{-1}) of the fungal pathogen *Beauveria bassiana* (Balsamo) Vuillemin (Ascomycota: Hypocreales) killed *H. axyridis*, whereas two other species included in the study (*A. bipunctata* and *C. septempunctata*) experienced high mortality (70% and 80% respectively) at a medium dose (10^7 spores ml^{-1}) of the pathogen. Koyama and Majerus (submitted to BioControl SI) found that *H. axyridis* had lower susceptibility than *C. septempunctata* to the parasitoid wasp *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae). Recent work on intraguild predation (Pell et al. submitted to BioControl SI; Roy et al. in press; Ware and Majerus submitted to BioControl SI; Ware et al. in press) indicates that *H. axyridis* will have a serious negative impact on native coccinellids in Europe.

Conclusion

We predict that *H. axyridis* will continue to spread in Europe, particularly northwards and eastwards. Northwards there are already initial records from Norway and Sweden, and whilst there is little evidence of establishment to date, this is likely in the near future. Spread into the Baltic states and Finland is also likely. Given that *H. axyridis* survives as a native species in parts of Siberia, the climate in these countries should not be a barrier to establishment. Eastwards it is entirely possible, (indeed likely), that the species is already present, but undetected, in countries such as Poland, Slovakia, Hungary and Slovenia. Ireland is the only remaining country left to be invaded from the westward spread, and we predict that *H. axyridis* will reach there, from Great Britain, in the relatively near future, and once established will spread across the whole country. The spread southwards is less certain, although as the species is adapted to Mediterranean and sub-tropical climates in parts of its native range (southern Japan and China), it may gradually adapt to the warmer climes of southern Europe, the Iberian peninsular and north Africa, and eventually establish and spread there. Indeed there are already initial reports of establishment in Egypt (S. Elnagdy, personal communication). Over a very short time period *H. axyridis* is likely to become one of the most widely distributed coccinellids in Europe. It remains to be seen what effect this will have on native coccinellids, but mounting evidence suggests a seriously detrimental impact.

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