

Predicting the potential geographical distribution of the harlequin ladybird, *Harmonia axyridis*, using the CLIMEX model

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Abstract *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) is a ladybird beetle native to temperate and subtropical parts of Asia. Since 1916 populations of this species have been introduced throughout the world, either deliberately, or by accident through international transport. *Harmonia axyridis* was originally released as a classical biological control agent of aphid and coccid pests in orchards and forests, but since 1994 it is also available as a commercial product for augmentative control in field and greenhouse crops. It is a very voracious and effective natural enemy of aphids, psyllids and coccids in various agricultural and horticultural habitats and forests. During the past 20 years, however, it has successfully invaded non-target habitats in North America (since 1988), Europe (1999) and South America (2001) respectively in a short period of time, attacking a wide range of non-pest species in different insect orders. Becoming part of the agricultural commercial pathway, it is prone to being introduced into large areas across the world by accident. We use the CLIMEX programme (v2) to predict the potential geographical distribution of *H. axyridis* by means of matching the climate of its region of origin with other regions in the world and taking in account biological characteristics of the species. Establishment and spread seem likely in many regions across the world, including those areas which *H. axyridis* has already invaded (temperate Europe, North America). Based on the CLIMEX prediction a large part of Mediterranean Europe, South America, Africa, Australia and New Zealand seem highly suitable for long-term survival of *H. axyridis* as

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well. In addition we evaluate CLIMEX as a strategic tool for estimating establishment potential as part of an environmental risk assessment procedure for biological control agents we discuss biological and ecological aspects necessary to fine-tune its establishment and spread in areas after it has been introduced.

Keywords *Harmonia axyridis* · Biological control · CLIMEX · Potential distribution · Climate matching

Introduction

The introduction of species into new regions of the world, either deliberately as a biological control agent or accidentally as a pest, can have a huge impact on agriculture and biodiversity. Before the import and release of any natural enemy as a biological control agent an environmental risk assessment can give an estimate of such an impact. van Lenteren et al. (2003) developed a methodology for assessing the risks of introducing biological control agents, which integrates information on the potential of an organism to establish, its dispersal capacities, its host range, and its direct and indirect effect on non-targets. The direct effects can be divided into effects on non-target herbivores, vectoring, and effects on other trophic levels such as intraguild predation, facultative hyperparasitism, and omnivory. The indirect effects can be divided into competition, indirect effects of intraguild predation, effects if the agent is a food source of another natural enemy, genetic changes due to hybridisation, linked trophic interactions, and non-food requirements like protection, pollination and (seed) dispersal. In such an environmental risk assessment procedure about establishment potential of a species introduced in a new region, is an important criterion (van Lenteren et al. 2003). Except using thermal data, such as cold tolerance and survival at low temperatures (Berthiaume et al. 2003; Hatherly et al. 2005), to assess the establishment potential in the area of release, modelling various stress parameters such as done by using the CLIMEX model may provide a reliable estimate of establishment potential for candidate non-native biological control agents outside its area of origin (Sutherst 2003; Sutherst and Maywald 2005).

Harmonia axyridis (Pallas, 1773) (Coleoptera: Coccinellidae), the harlequin ladybird, is a ladybird beetle native to continental, temperate and subtropical parts of east and central Asia (Iablokoff-Khnzorian 1982). Since the beginning of the 20th century this species has been introduced several times as a biological control agent into different parts of the world. In North America, South of Europe and the Soviet Union it has been released in classical biological control programmes against aphid and/or coccid pests. Since the mid 1990s *H. axyridis* has been offered as a commercial biological control agent in Europe for aphid control in greenhouse and urban ecosystems, and multiple releases have been made for a 1–2 decades in several countries. First records of establishment outside its native range took place in North America in 1988 (Chapin and Brou 1991), in Europe in 2000 (Bathon 2002) and South America in 1998 (Saini 2004). Gradually *H. axyridis* has expanded its range across these continents by natural dispersal during fall, spring and summer, or is currently doing so. In North America *H. axyridis* has spread across the east coast within 5–6 years time (Koch et al. 2006). *H. axyridis* is showing two kinds of migratory behaviour: autumn and spring migration to and from overwintering sites, and summer migrations when food sources are scarce. These summer migrations are random in direction, but often wind-driven. The autumn migrations on the other hand are not random, but directional away from the afternoon sunlight (Lo and Liu 1976; Nalepa et al. 2005),

i.e. heading to the northeast. Likely the spring migration, when adults leave their overwintering sites and return to foraging areas, is directional as well, but no data are available for this. Besides intentional introductions, accidental introductions may have taken place as well, as a result of increase in international trade. Eggs, pupae, larvae and adults may be carried as a stow-away in ships and airplanes when attached to leaves, branches and trunks of potted plants, trees, and shrubs. On Tenerife, the Canary Islands, a single specimen was found in the autumn of 2003 and again in 2004 (Machado 2006). In the UK specimens have been intercepted from transatlantic produce in 2004 (Majerus et al. 2006), and in Norway on horticultural produce from the Netherlands in 2006 (Arnstein Staverløkk, personal communication 2007).

What characteristics make *H. axyridis* a successful invader? First, it is known from a large native geographical area, with a wide variety of phenotypes, that differ both within populations and geographic location (Mader 1926–1937, Dobzhansky 1933). Grill et al. (1997) showed that *H. axyridis* displays phenotypic plasticity in several characters important for successful colonization of a new area, e.g. the ability to adapt to a wide range of climates. Secondly, *H. axyridis* has a strong potential to spread by flight, by accidental introductions, and through commercial releases. Thirdly, *H. axyridis* has a wide food range and consumes all kind of soft-bodied insects of many taxa besides aphids, its main prey (Iablokoff-Khnzorian 1982). *Harmonia axyridis* reproduces in a wide range of habitats, whereas many native coccinellids tend to be more habitat- and niche-specific (Majerus et al. 2006). It is also able to reproduce during a long time of the year: the adults become active early in the season (April) and larvae and pupae still can be found in November (Majerus et al. 2006). Being a successful invader could also mean that it has an adverse effect on native aphidophagous predators (e.g. Lanzoni et al. 2004). Cannibalism and intraguild predation are common, and several sources (e.g. Brown and Miller 1998; Colunga-Garcia and Gage 1998; Snyder et al. 2004) report a decline of the population of native aphidophagous ladybeetles that can lead to displacement of native species.

In this paper we use climate scenarios from the simulation software CLIMEX 2.0 to predict the establishment potential of *Harmonia axyridis* in new areas of introduction of the world and verify the outcome by visually matching its current presence in newly invaded areas. We also evaluate CLIMEX as a strategic tool for establishment potential and environmental risk assessments of biological control agents and rapid decision making.

Material and methods

The CLIMEX model

In this study we used the CLIMEX model for Windows Version 2 (Sutherst et al. 2004) to develop a model of climatic responses of *H. axyridis* based on its recorded distribution. The best way to make a prediction is to use the native distribution as a basis for fitting the model parameters. CLIMEX uses climatic responses of an organism and meteorological data to predict the potential distribution and relative abundance of poikilothermic organisms under current climatic conditions. Predictions can be made on a world scale or on a regional scale (Sutherst et al. 2004). In CLIMEX over 2000 locations (meteorological stations) worldwide are included. The climatic data associated with these locations span the period 1960–1990 (Müller 1996).

For a simple comparison of meteorological data at different locations, the function ‘Match Climates’ can be used, e.g. for targeting collection sites of new, unknown biological

control agents, adapted to a certain area of release (e.g. performed by Koch et al. (2006) for South America) but it does not take species characteristics into account. Here, we used this function for targeting the collection sites that could have been the source area of releases in Europe and North America. A second function, the species-specific response (CLIMEX) model, however, allows the user to predict the potential geographic distribution of a given species based on its biology and long-term meteorological data ('Compare Locations'). Species parameters are part of the input in the CLIMEX model, and describe a species' response to climate (Sutherst et al. 2004). These parameters are divided into three groups: one group defines seasonal population growth, another defines stresses (cold, hot, wet and dry) that limit the geographical distribution, and the third describes the limiting conditions that may exclude species from some areas. The probability that the populations can survive under unfavourable conditions is described by these parameters. From these parameters the growth index (GI) and stress temperature and moisture indices (TI, MI) are calculated weekly, and can be combined into an overall annual index of climatic suitability, the ecoclimatic index (EI). Scaled from 0 to 100 it is a measure of climatic suitability for the species concerned. A location can only have an EI of 100 when that location provides ideal conditions, without stress, throughout the year. In temperate areas or regions with distinct stressful wet and dry seasons the maximum EI would be around 50. Values of >20 already have been found to support substantial population densities (Sutherst 2003).

A species' behaviour in a CLIMEX simulation depends on the parameter values. The values of the species parameters are based on seasonal distribution data and experimental observations on developmental threshold temperatures and moisture levels. The more values of a parameter are known, the more reliable the picture (map of potential species distribution) in CLIMEX will be. If some values of the species parameter are missing, values of the parameter templates can be used. Once the species' parameter file has been adequately defined as a starting set of parameter values, the 'Compare Locations' function helps the user to fit the parameters. During the iterative adjustments-and-comparison process the parameter values for *H. axyridis* change to visually fit the observed native geographic distribution.

Native geographic distribution

Harmonia axyridis has its origin in the east of the palaeartic region. Its distribution ranges from the Altai mountains in the west to Japan, Yeniseisk (Krasnoyarsk) in the north, Sakhalin and the Kurile Islands in the east and Guanxi (China) in the south (Dobzhansky 1933; Komai et al. 1950; Iablokoff-Khnzorian 1982; Kuznetkov 1997) (Fig. 1). Several sources indicate its presence in Taiwan (CABI/EPPO 2007; Poorani 2004), but Sasaji (1982) states that the observations and collected specimens did not concern *H. axyridis*, but *Harmonia yedoensis* (Takizawa). The records from the Himalaya and/or Nepal (Iablokoff-Khnzorian 1982; Poorani 2004) need confirmation because these papers are the only, but not original records. Also records from certain areas in Russia, as cited by CABI/EPPO (2007), are not supported by the underlying original papers and would need confirmation.

Fitting parameters

There was a large degree in similarity between the potential distribution generated by the temperate template in the CLIMEX model and the native range of *H. axyridis* in Asia. We

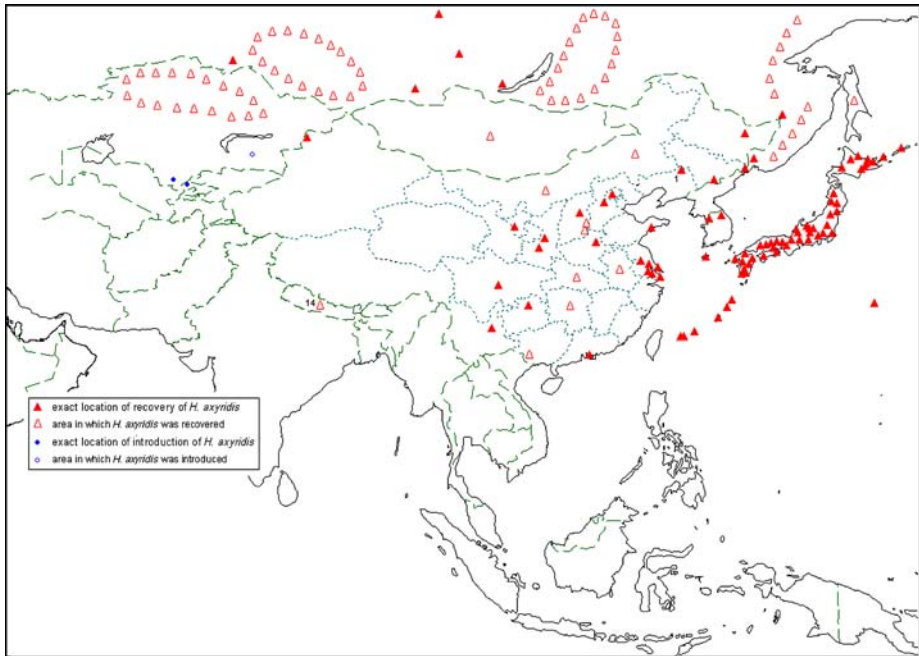


Fig. 1 Distribution of *Harmonia axyridis* in Asia (based on CABI/EPPO 2007; Komai et al. 1950 and others, corrected and modified)

therefore used that template as the starting point for our iteration process. In the next paragraphs we discuss what experimental values we used in the model.

Temperature

DV parameters are the limiting and optimal temperatures for population growth of a species. DV0 and DV3 are the limiting low and high temperatures respectively, at or below and above no population growth takes place. DV1 and DV2 are the lower optimal and upper optimal temperature respectively. Population growth of a species is reduced if the ambient temperature is below DV1. No population growth takes place when the ambient temperature equals or exceeds DV3. DV0 is not exactly equivalent to a developmental threshold for any life stage, but the temperature threshold for population growth, which is at best established under field conditions. Experimental values for DV0 (limiting low temperature) range from 9.3°C (pre-oviposition period) (Soares et al. 2003) to 13.3°C (pupa) (cited in Hodek and Honěk 1996). In this study 10.5°C was adopted for DV0 (Schanderl et al. 1985). Three sources of optimal temperatures have been found. Soares et al. (2003) found 20°C to be the lower optimal temperature DV1, and 25°C for the upper optimal temperature DV2. Barçın et al. (2001) found values for these two parameter of 15°C and 25°C respectively. Yuan et al. (1994) found values for the optimal temperature for adult development of 23–25°C. In this study 15°C is adopted for DV1, and 25°C for DV2. The highest limiting temperature DV3 values found in literature varied between 30°C and 35°C (Barçın et al. 2001; Michaud 2002). In this study DV3 was set to 35°C.

The rigour of an unfavourable season is not the only way in which climate can limit a species' distribution. It may also be necessary to have enough thermal accumulation during the growth season to enable the species to complete a minimum amount of development. PDD is the minimum number of degree-days above DV0, necessary to complete a generation of an organism. If the number of degree-days set for PDD is not reached at a certain location the ecoclimatic index (EI) is set to zero (cross on the maps), and the species is excluded from this location. Thermal constants for a complete life-cycle were not found. Only thermal constants of the egg stage, larval stage and pupal stage were found and ranged from 231.3 (egg-to-adult) (Schanderl et al. 1985) to 267.3 (LaMana and Miller 1998). Because the pre-oviposition period is missing in the calculation of these degree-days, the PDD value was set to 330 to make the life cycle complete.

Moisture

SM parameters are the soil moisture indices for population growth of a species. SM0 and SM3 are the limiting low and high index respectively, at or below and above no population growth takes place. SM1 and SM2 are the lower and upper optimal index respectively. Population growth of a species is reduced if soil moisture is below SM1. No population growth takes place when soil moisture equals or exceeds SM3. Values for soil moisture in relation to the performance of *H. axyridis*, a leaf and branch foraging predator, are of indirect importance through host plant growth and availability of suitable prey. In this study the SM-values from the temperate template were used as the start (SM0: 0.25; SM1: 0.8; SM2: 1.5; SM3: 2.0). Initially, irrigation was not included in the model.

Diapause

During winter, adults of *H. axyridis* exhibit diapause (Nalepa et al. 1996). In late winter or early spring, the beetles switch from diapause to a quiescence state. Preceding diapause the beetles are migrating to their overwintering habitats. In Asia the migration from feeding habitats to overwintering habitats occurs from mid-October to late November. During these migration flights the beetles fly towards prominent, isolated objects such as mountaintops and buildings and land on surfaces, like rocks or walls, that are often white or lightly coloured (Lo and Liu 1976, Nalepa et al. 2005). Little is known about the distance covered between the feeding habitat and the overwintering habitat though observations on winter aggregations suggest they may not travel long distances during that period (Nalepa et al. 1996). Overwintering sites are mountain cleaves, but also houses or other buildings. Like other coccinellids, *H. axyridis* forms mass aggregations at the overwintering sites. During summer beetles may become quiescent and aestivate, although nothing is known about the conditions at which this occurs. DPD0 and DPT0 are the diapause induction day length and the diapause induction temperature respectively. DPT1 is the diapause termination temperature, for winter diapause the minimum temperature that determines it. DPD (diapause development days) is the minimum number of days below DPT0 required for diapause development to be completed. DPSW is an indicator for summer or winter diapause, to be set to 1 or 0 respectively. *Harmonia axyridis* enters diapause in the adult stage. No exact values for the diapause induction day-length and diapause induction temperature have been

found in literature. From several sources a value of 12 h, and 16°C and 18°C could be traced for the diapause induction daylength and temperature (Sakurai et al. 1988). In this study a value of 12 is adopted for DPD0 and 16 for DPT0. No general value could be found for the diapause termination temperature. Soares et al. (2001) found different values for the adult lower developmental threshold for the phenotypes 'aulica' and 'nigra': 9.3°C and 10.4°C, respectively. In this study 9.3°C was initially adopted for the DPT1. Values for DPD (diapause development days) were not found in literature. In this study a value of 0 is initially adopted for this parameter.

Light

In the model, LT0 is the day-length above which growth is at a maximum, and LT1 is the day-length below which growth is zero. No data on day-length was found in literature, so LT-values were not used in this study.

Stress

Stress parameters are set to a species' ability to survive adverse seasonal conditions, and so determine its geographical distribution. Stress, leading to negative population growth, is assumed to accumulate outside the values of DV0 and DV3 (temperature limits) and of SM0 and SM3 (moisture limits). Accordingly, there are four kinds of stress: cold, heat, dry and wet stress. Cold and heat stress can occur in two different ways. In the degree-day model, it is assumed that cold stress occurs because the seasonal thermal accumulation is too low to complete the life cycle. In case of heat stress it is assumed that the daily heat load is too high for the essential physiological processes. In the lethal temperature method, stress occurs in response to excessively low minimum temperatures or high maximum temperatures. Both types of stress may occur for the one species. In this study the stress temperature threshold method is used. From survival time data at -5°C to 5°C , Watanabe (2002) found that in Japan the optimum temperature for overwintering is between 0°C and -5°C . Berthiaume et al. (2003) found similar results for Canada, but recorded a significant decrease in survival at -10°C . A value of 0°C was initially adopted for TTCS (cold stress temperature threshold). TTHS (heat stress temperature threshold) was set to 35°C . Information on the rate of heat and cold stress accumulation (THCS, THHS) as well as on dry and wet stress parameters was not found in literature, so values of temperate template were adopted (THCS: 0°C ; THHS: 0.005°C). Interactions of stress indices were not found in literature, so these parameters were not used in this study. When no specific value could be found in literature for some parameters of the model, we used values estimated from the temperate template.

Experimental values of temperature-moisture- and diapause-related parameters mentioned above were included in the CLIMEX model and estimated visually by iteration, using the known Asian distribution of *H. axyridis* as a reference. Parameter values used are shown in Table 1. These CLIMEX parameter values were then applied to meteorological data from stations across the world and we visually compared the similarity between the predictions made in CLIMEX and the current distribution of *H. axyridis* in newly invaded areas (North America, Europe, South America). After that we performed a sensitivity test of parameter values for these areas to verify the fit.

Table 1 CLIMEX parameters settings *Harmonia axyridis*

Code	Parameter description	Values	
		Before iteration	After iteration
<i>Temperature</i>			
DV0	Limiting low temperature (°C)	10.5	10.5
DV1	Lower optimal temperature (°C)	15	15
DV2	Upper optimal temperature (°C)	24	25
DV3	Limiting high temperature (°C)	35	35
PDD	Minimum degree-days above DV0 (DD)	330	330
<i>Moisture</i>			
SMO	Limiting low moisture index	0.25	0.1
SM1	Lower optimal moisture index	0.8	0.3
SM2	Upper optimal moisture index	1.5	1.9
SM3	Limiting high moisture index	2.0	2.0
<i>Diapause</i>			
DPD0	Diapause induction day length (h)	12	14
DPT0	Diapause induction temperature (°C)	16	16
DPT1	Diapause termination temperature (°C)	9.3	7.3
DPD	Diapause development days (days)	0	40
DPSW	Summer/winter diapause	0	0
<i>Stress</i>			
TTCS	Cold stress temperature threshold (°C)	0	-5
THCS	Cold stress temperature rate	0	0.00002
DTCS	Cold stress degree-day threshold (DD)	0	0
DHCS	Cold stress degree-day rate	0	0
TTHS	Heat stress temperature threshold (°C)	35	35
THHS	Heat stress temperature rate	0.005	0.005
DTHS	Heat stress degree-day threshold (DD)	0	0
DHHS	Heat stress degree-day rate	0	0
SMDS	Dry stress threshold	0.2	0.01
HDS	Dry stress rate	-0.005	-0.001
SMWS	Wet stress threshold	2	2
HWS	Wet stress rate	0.002	0.01

Results

The iteration process

During the iterative adjustments-and-comparison process for *H. axyridis*, values of some parameters had a large effect on the EI and therefore on the potential distribution. The CLIMEX parameter values that gave the closest visual fit between the known (Fig. 1) and predicted (Fig. 2) distribution in Asia are shown in Table 1. During the iteration process, diapause showed to be the key factor for the absence of positive EI-values of *H. axyridis* in the north and in the south. When iterating the values of the diapause parameters, the diapause termination temperature (DPT1) was the key factor for explaining the absence of

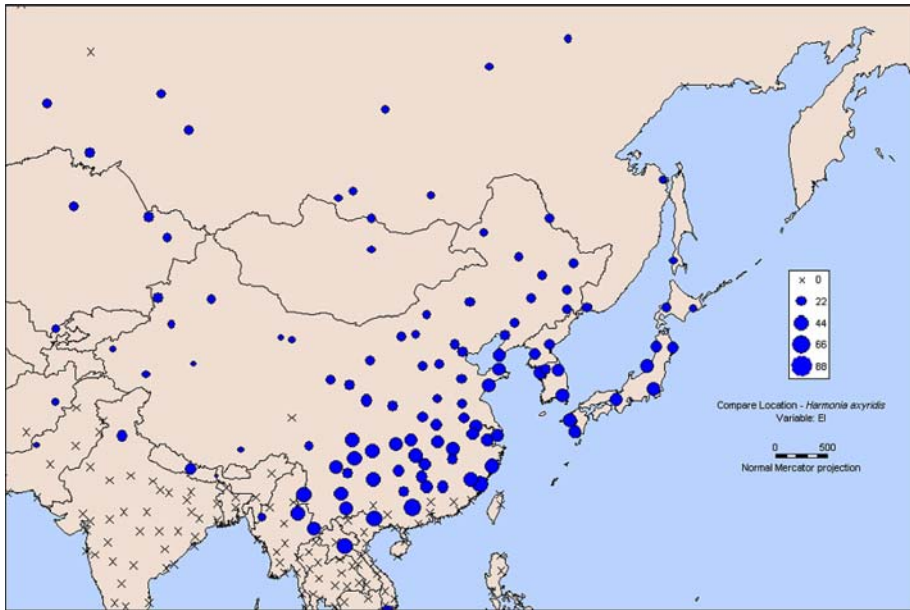


Fig. 2 CLIMEX map of Asia indicating Ecoclimatic Indices (EI). Crosses represent an EI of zero. Spots represents EI's greater than zero. The larger the spot the larger the EI and the more suitable the climate at that station

EI-values in the north. We therefore downgraded the value of this parameter from 9.3°C to 7.3°C to match its presence in South Siberia e.g. Irkutsk, from where *H. axyridis* is known to occur (Fig. 1). On the other hand, the diapause development days (DPD), the minimal number of days necessary to end the state of diapause, showed to be the critical parameter in explaining the southern edge of its native area of distribution. When iterating parameter values ranging between 0 day (no diapause) and 180 days (obligate diapause), a minimal value of 40 day gave the best visual fit, matching south Chinese records in Yunnan (Kuang and Xiao 1995) and in Guang near the Vietnamese border (CABI/EPPO 2007). Temperature and soil moisture parameters largely affected the value of the EI for *H. axyridis*, but was much less limiting in matching its distribution potential as diapause. Stress factors (dry, wet) proved to be of little or no importance on the outcome of the model: cold stress values (CS) remained below a value of 25 (of 100) for populations in the north, but heat stress values increased from Beijing towards the south of China (HS 12–75). Besides climatic suitability, the occurrence of *H. axyridis* depends on humidity through food availability. Its prey, primarily aphids, often occur in areas where irrigation is applied. A 2 mm summer irrigation application per day, after checking several values (0–10 mm), gave the best fit.

When we applied these parameters (Table 1) to meteorological data from stations across the world within CLIMEX, the map of EI's on a worldwide scale suggests that a large part of the global climate is suitable for establishment of *H. axyridis* (Fig. 3). For Europe (Finland) and North America (Alaska) the potential northern distribution limit of *H. axyridis* lies somewhere at 64°N , whereas its most northern record in Siberia (Yeniseisk/Krasnoyarsk) is from 58°N . In North America the eastern part of the continent is suitable for survival on a long-term scale. In the western part of the continent the EI values are

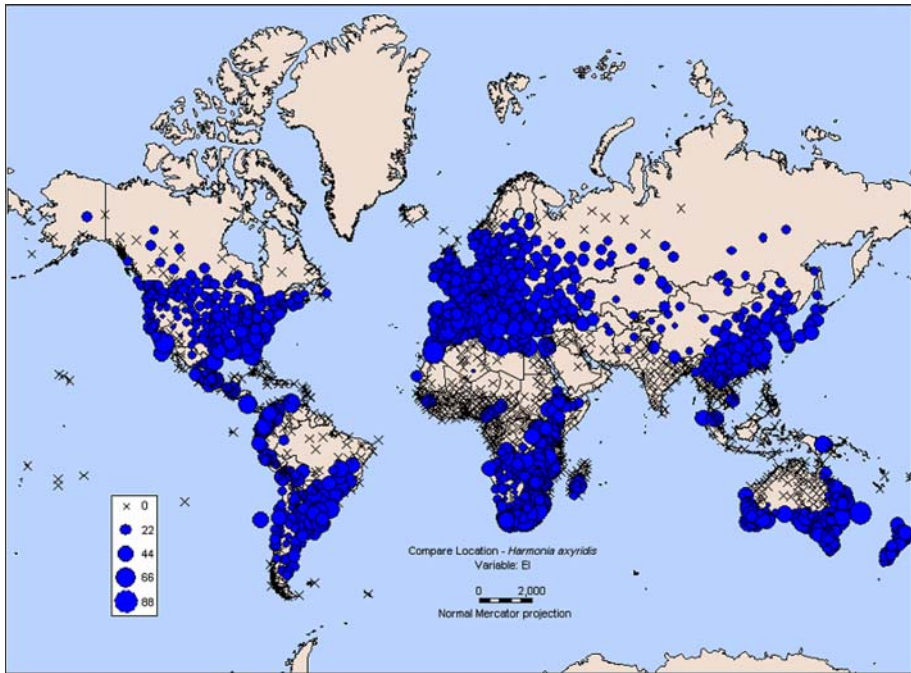


Fig. 3 CLIMEX map of the world indicating Ecoclimatic Indices (EI). Crosses represent an EI of zero. Spots represents EI's greater than zero. The larger the spot the larger the EI and the more suitable the climate at that station

smaller for the inland regions, and higher for the coastal regions (Washington, Oregon and California) (Fig. 4). In Europe concentrations of high EI scores (16–72) are shown for the whole European continent, except for the northern part of Scandinavia and Iceland (Fig. 6). For both continents, dry and wet stress factors were of minor importance, whereas cold and heat stress determined the GI value and therefore the ecoclimatic index EI in the north and south respectively. In particular, changing DPD values (from 40 to 90 days or more) for Europe and North America largely affected the outcome of the EI values in the south and therefore shifted the area of potential distribution towards the north, giving an even better fit.

Match with current geographic distribution

Harmonia axyridis has been introduced several times for classical biological control purposes in North America in the beginning of the 20th century (Table 2). These introductions did not result in any known establishment. From 1978 till 1985, series of releases were made with *H. axyridis* for the control of aphid species like *Monellia caryella* (Fitch) and coccids like *Matsucoccus resinosae* Bean and Godwin (Gordon 1985). Populations from different origins in Asia were released in several states (ARS 2005): Japan (Washington, Delaware), South Korea (Connecticut, Georgia, Maine and Maryland), Russia (Delaware, Maine, Maryland, Mississippi and Nova Scotia-Canada). In addition, releases have been made later on in several areas in Mexico (cited in Koch et al. 2006). The first

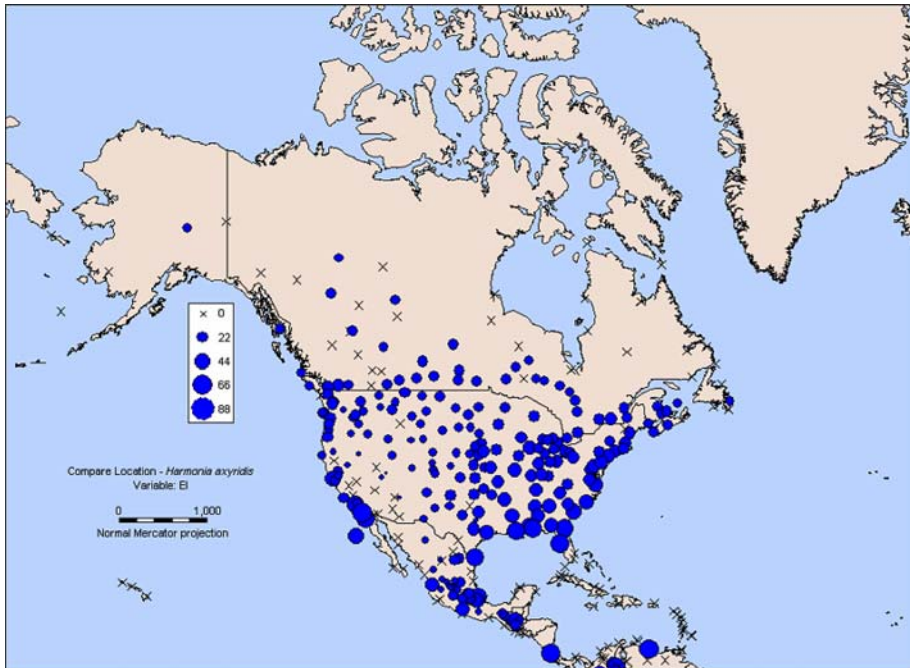


Fig. 4 CLIMEX map of North America indicating Ecoclimatic Indices (EI). Crosses represent an EI of zero. Spots represents EI's greater than zero. The larger the spot the larger the EI and the more suitable the climate at that station

feral record in North America was made in 1988 was by Chapin and Brou (1991). Subsequent records were made at three widely separated locations in northern and southern Mississippi, and in northern Georgia in 1990 (Chapin and Brou 1991; Tedders and Schaefer 1994) and in northern Alabama in 1991 (Day et al. 1994). From there *H. axyridis* has spread throughout Georgia, northern Florida and eastern South Carolina in 1992, reached Virginia in early 1993, and by fall 1993 it was collected farther north, in Delaware, Pennsylvania, and New Jersey (Tedders and Schaefer 1994; Day et al. 1994) and in 1993–1994 all of the states east of the Mississippi were invaded, as well as California, Oregon and Washington on the west coast. From 1994 onwards *H. axyridis* was recorded in Canada as well and is now widely established in North America (Fig. 5) (Koch et al. 2006). When visually comparing the predicted (Fig. 4) and realized (Fig. 5) distribution in North America there is a close fit between both distributions, except for the most northern Canadian stations.

In Europe, *H. axyridis* was first introduced from the Far East (Primorskyi (Vladivostok)) as a classical biological control agent in Georgia in 1927 (Iablokoff-Khnzorian 1982), in the Ukraine from 1964 till 1971 (Koval and Zderchuk 1973), in Kazakhstan in 1968 (Savoiskaya 1970), and in Belarus (Sidlyarevich and Voronin 1973) (Table 3). These introductions, however, did not result in establishment of the species. A second introduction was made by the French National Institute for Agronomical Research (INRA) in 1982 using a population from China (Iperti and Bertrand 2001). It was kept in quarantine till 1990, after which experimental field releases were made in France from 1990 onwards. As far as currently known, most releases in western Europe have been made with offspring

Table 2 Introduction of *Harmonia axyridis* in North America (after Gordon 1985, and ARS 2005)

Place of origin	Year of import	Year of introduction	Place of introduction	Establishment from release	Reference
?	1916		Hawaii	Unknown	Iablokoff-Khuzorian (1982)
China	1927	1927–1928	Florida	No	Watson (1929)
Japan	1916, 1964	1916, 1964, 1965	California	No (Gordon 1985)	Chant (1964, 1965); Essig, 1931 (in Gordon 1985)
Japan (Fukuoka)	1978	1978–1982	Washington, Delaware	Unknown	ARS (2005); J. Coulson, in Gordon (1985)
Japan	1978	>1978	Georgia (Houston: Perry; Peach: Byron)	No (Gordon 1985)	R. Dysart, in Gordon (1985)
Former USSR (Primorskiy Kray: Ussuriysk)	1978	1981	Nova Scotia	Unknown	R. Dysart, in Gordon (1985)
Former USSR (Primorskiy Kray: Ussuriysk)	1978–1984	1978 onwards	Connecticut (New Haven: Mt Carmel-Lockwood), Georgia, Louisiana, Maryland (Prince Georges: Beltsville), Washington D.C., Delaware, Maine (Hancock: Catherine Hill Mtn.), Mississippi (Washington: Leland and Stoneville), Ohio, Pennsylvania	Unknown	ARS (2005); R. Dysart, in Gordon (1985)
Japan	1979	1979, 1980	Louisiana, Mississippi (Washington: Leland and Stoneville)	Unknown	Chapin and Brou (1991); Tedders and Schaefer (1994)
South Korea	1981	1981–1985	Connecticut, Georgia, Maine and Maryland	Unknown	ARS (2005)

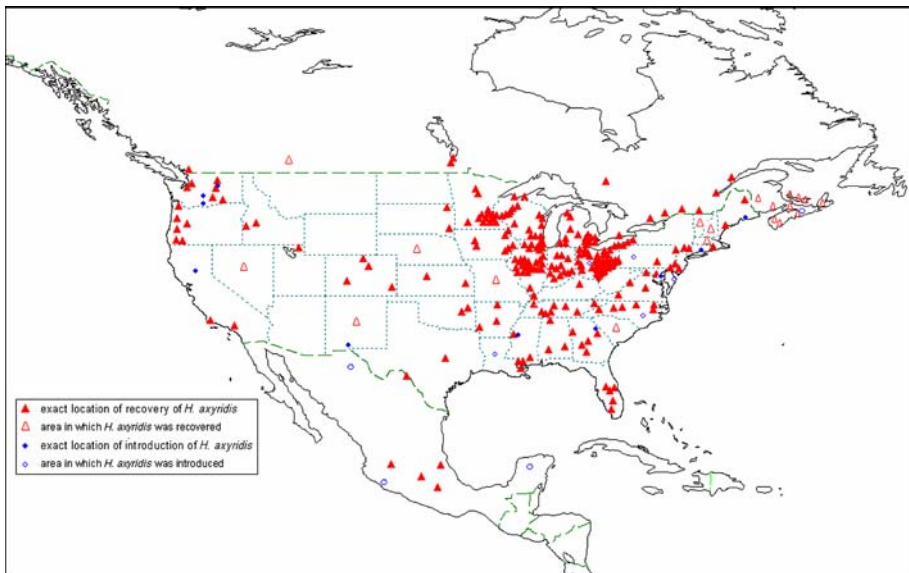


Fig. 5 Distribution of *Harmonia axyridis* in North America (based on CABI/EPPO 2007, and Koch et al. 2006)

of the INRA source population: as a biological control agent of *Toxoptera citrida* in citrus in Portugal (Azores: Garcia 1986) in 1984, and in Greece in 1994 (Katsoyannos et al. 1997), and for aphid control outdoors in France since 1993 (Kabiri 2006). From the mid 1990s onwards biocontrol companies have commercialized *H. axyridis* as a commercial product for aphid control in augmentative biological control programmes indoors. Commercial releases were made in western Europe from 1993 onwards, in France (1993: Kabiri 2006), Belgium (1996: Adriaens et al. 2003), the Netherlands (1995: Cuppen et al. 2004), Italy (1996: Orlandini and Martellucci 1997) and has been offered commercially for a few years or more in most other European countries as well. It has never been sold officially in Germany, UK and Switzerland.

The first feral aggregation in Europe was observed during the winter of 1999–2000 on a balcony in a Frankfurt (Germany) suburb (Bathon 2002). Subsequent feral populations were recorded from Belgium in 2001, the Netherlands in 2002 (Cuppen et al. 2004), France in 2003 (Kabiri 2006), Luxemburg in 2003 (Schneider and Loomans 2006), United Kingdom in 2004 (Majerus et al. 2007), Switzerland in 2004 (Klausnitzer 2004), Austria in 2006 (Rabitsch and Schuh 2006) and Czechia (Brown et al. 2007) (Fig. 7). Kangas (1945) reported *H. axyridis* from Finland, but after studying the specimen (Loomans, personal observation 2007), it turned out to be *Harmonia conformis* (Boisduval). Large numbers are nowadays regularly observed in the Netherlands, Belgium, Luxemburg, Germany, northern France and UK. In South-European countries *H. axyridis* has been recorded, but only incidentally and in low numbers (e.g. Katsoyannos et al. 1997). Other releases in the Westpalaearctic region are known from Egypt and Syria (Abdel-Salam and Abdel-Baky 2001: origin USA; but also China (INRA)) (Table 3). When we compare the potential (Fig. 6) and realized (Fig. 7) distribution in Europe and North Africa there is not as close a fit between both distributions as for North America, but the current area of distribution falls within the predicted range.

Table 3 Introductions of *Harmonia axyridis* in Eurasia

Region of origin	Year of import	Year of introduction	Place of introduction	Establishment from release	Reference
Eastern Maritime Territory (Primorsky Krai)	1964	1964	Ukraine (Chernovitskaya)	Unknown	Koval and Zderchuk (1973); Sinadskii and Kozarzhhevskaya (1980); Voronin (1968)
Eastern Maritime Territory (Primorsky Krai)	1969	1969	Ukraine (Crimea)	Unknown	Savoiskaja (1970)
Eastern Maritime Territory (Primorsky Krai)	1969	1969	South-eastern Kazakhstan	Unknown	
Belarus	1968	1968–1970	Minsk, glasshouse release	Unknown	Sidlyarevich and Voronin (1973)
China	1982	>1993	France	Unknown	Ongagna et al. (1993); Kabiri (2006)
China ^a	1984	1984	Azores Islands		Garcia (1986)
China ^a	1993	1994	Greece	Yes	Katsoyannos et al. (1997)
China ^a	1995	1996	The Netherlands	Yes	Cuppen et al. (2004)
China ^a	1995	1997	Belgium	Yes	Adriaens et al. (2003)

^a distributed by INRA and Biotop

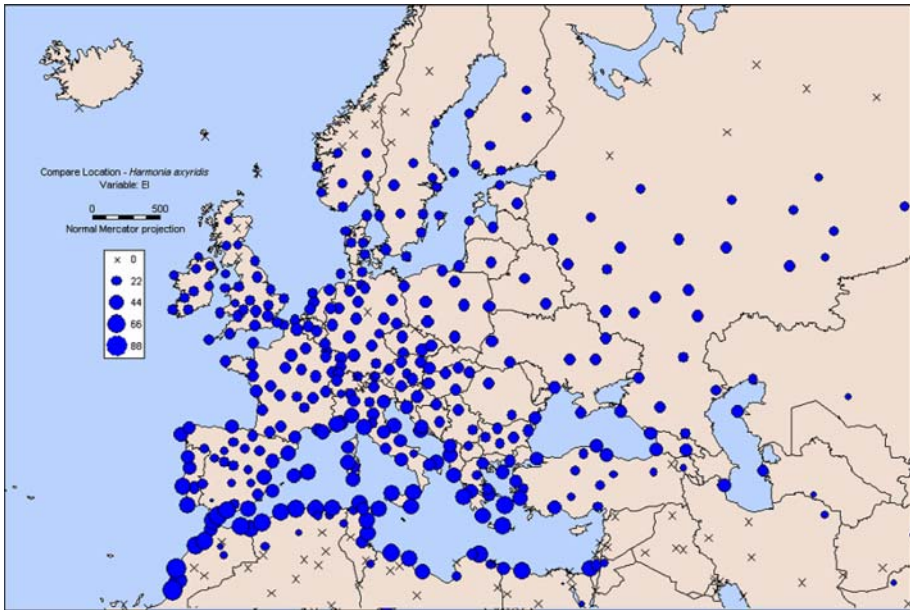


Fig. 6 CLIMEX map of Europe and northern Africa indicating Ecoclimatic Indices (EI). Crosses represent an EI of zero. Spots represents EI's greater than zero. The larger the spot the larger the EI and the more suitable the climate at that station

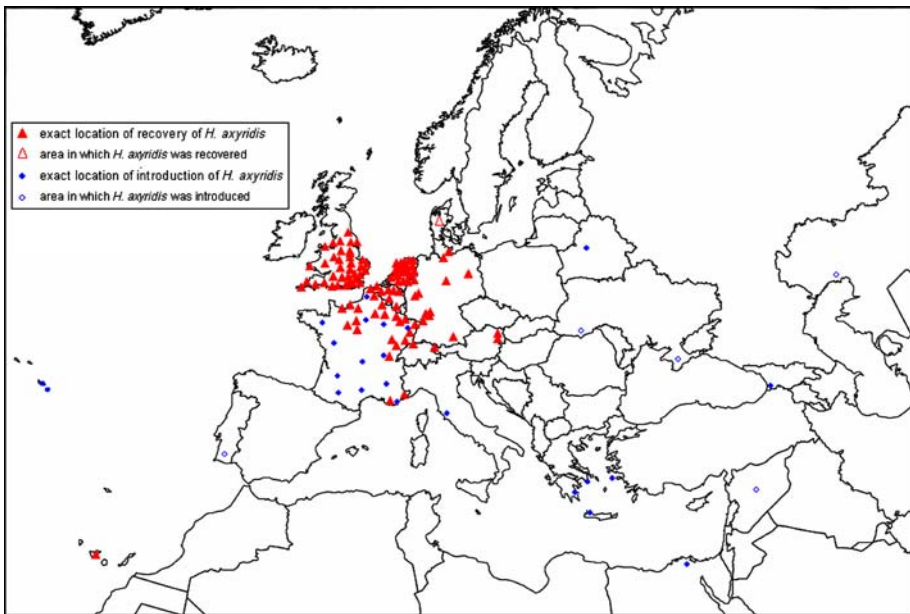


Fig. 7 Distribution of *Harmonia axyridis* in Europe and northern Africa (based on CABI/EPPO 2007, corrected and modified)

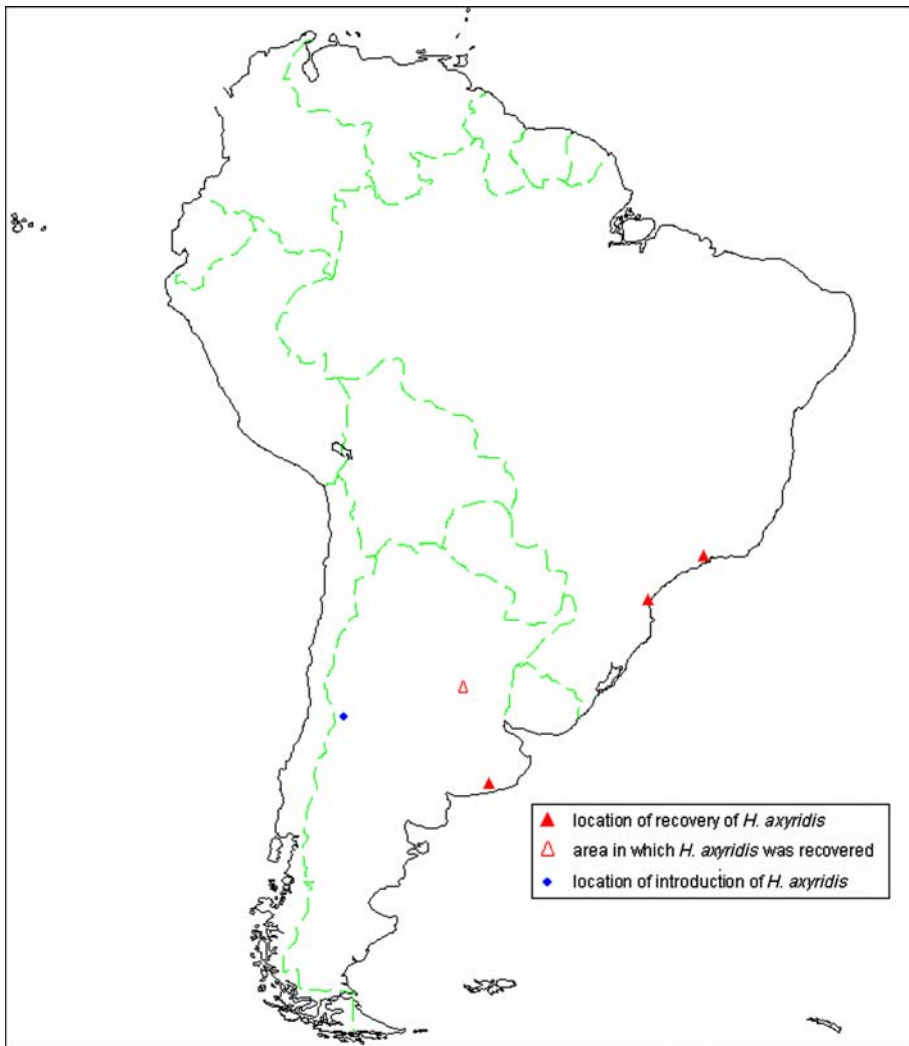


Fig. 8 Distribution of *Harmonia axyridis* in South America (after Saini 2004 and author's information)

In South America *H. axyridis* has been introduced through INRA in Mendoza—Argentina in 1986, 1987 (García et al. 1999) and 1999 (Saini 2004) and in a few years time it has spread into a large part of that country (Fig. 8). Since 2001 it is found in the Buenos Aires area (Saini, 2004) and south of there. In Brazil *H. axyridis* has never been released but was recorded from Curitiba in 2002 (de Almeida and Da Silva 2002) and Sao Paulo in 2007 (Enio Branco, personal communication 2007). Introduction and spread into South America is quite a recent date, and *H. axyridis* may still expand beyond its current range. Other regions on the southern hemisphere, like Africa, Australia and New Zealand, that according to the outcome of the CLIMEX model would be suitable for long-term survival of *H. axyridis* (Fig. 3), would be under threat.

Discussion

The output of a CLIMEX run using several indices for a single location, are integrated into one index (EI) that will indicate the long-term survival of a particular species on that location (Sutherst 2003). The strength of CLIMEX 'Compare Locations' is that it combines the freestanding climatic data, like temperature, precipitation, and relative humidity and integrates these with the biological characteristics of species and shows the indices for long-term survival of all the locations in one glance. CLIMEX has shown to be an effective tool for predicting the distribution and assessing the risks of a large range of species, plant pests as well as natural enemies (Sutherst and Maywald 2005). The current analysis projects the potential geographic distribution of *H. axyridis* in various parts of the world, based on fitting of CLIMEX parameters. Simulated trends show that, for those areas where *H. axyridis* already has been introduced, established and spread, its predicted distribution is largely supported by field data: there is a great consistency between the predicted and realized distribution in North America (Fig. 4, 5) and in Europe (Fig. 6, 7). Predictions for its northern and southern range in North America and Europe are not (yet) completely covered by the actual records. The accuracy of this prediction using the CLIMEX model can be divided in model-based factors and species-based factors. Below we discuss what factors are involved and what experimental data would be needed to verify and specify the model and the accuracy of its use.

Model based factors

Climatic suitability versus actual distribution

As every simulation program for ecological phenomena, CLIMEX has its limitations. Climate models greatly rely on the number and distribution of meteorological stations: the network is not equal per region and is rather low in northern parts of the world, where there are few inhabitants. Areas with a small number of stations may not give a representative view of the climate in that region, because the location of the meteorological stations is frequently unrepresentative for the surrounding area (Bennett et al. 1998). CLIMEX records the presence or absence of a given species, but does not include a measure of abundance, that allows favourable areas to be distinguished from marginal areas. CLIMEX works with climatic data and climate related species characteristics only, and it works with the assumption that the range of a species is solely determined by climate. Within the climatic range of a species also non-climatic factors will of course limit its potential distribution as well, acting individually or in combination (Baker et al. 2000). These physical and biological factors, such as soil type, availability of food and substrates for specific developmental processes (e.g. larval development, overwintering), dispersal capacities of the species, and interactions between species, such as competition, predation and parasitism as well as existing pest management practices are not included in CLIMEX simulations (Baker et al. 2000). Northern regions like central Canada and the Great Plains in the USA are mostly cultivated and have flat terrain and overwintering sites are limited to trees and aggregations are subject to extreme cold when not able to shelter. This could partly explain why these regions have low or no distribution records (Fig. 5), while the model predicts a significant EI value (Fig. 4). Extreme climatic conditions such as cold winters, however, could prevent that *H. axyridis* from establishing.

Species based parameters

Input biological species characteristics

Several factors (species parameters) will affect the potential distribution as indicated by the CLIMEX map, but eventually one of these factors acts as the limiting factor, though another may become limiting as other species parameter values change. CLIMEX predictions are only based on the long-term survival of species on locations during the whole year. To what extent *H. axyridis* is able to build up seasonal populations beyond its overwintering range and can cause severe impact during the growing season, is not clear.

Genetic differences

The observed geographical distribution of a species reflects the sum of all the genetic variation contained in that species (Sutherst et al. 2000). When a species like *H. axyridis*, however, has been introduced into a new area only a small proportion of the gene pool has been used. Consequently, the founder individuals may produce populations that may have characters that differ from the mother population (Samways 2003). Specimens of different populations of a species with a great native distribution range could react differently to climate, caused by the genetic differences between the geographically widely separated populations. The different populations and phenotypes of *H. axyridis* could have different adaptations to climate (Kuang and Xiao 1995) and season (Osawa 2001). Therefore, it is not always safe to assume that a small proportion, which is used in research, is representative for the whole population. Because of this, the species parameter values should be used as an indication, and can be modified if the potential distribution will not fit the actual distribution range. However, the more observations and species parameter values are introduced, the more reliable the picture will be.

Harmonia axyridis is widespread throughout temperate and subtropical Asia and geographical genetic polymorphism could occur in their response to climatic cues. The elytral pattern polymorphism shows a distinct geographical pattern (Mader 1926–1937; Dobzhansky 1933, Komai et al. 1950) and is caused by different factors, including climate, food sources, and genetic components. The macro-geographical variations are mostly related to climatic factors, while micro-geographic variations are mostly related to food availability (Muggleton 1978; Soares et al. 2003). Within populations there are also seasonal variations in the proportions of the light and dark coloured individuals. Research by Osawa and Nishida (1992) showed an increase in the frequency of the ‘succinea’ phenotype from spring to summer in relation to non-random mating among the different phenotypes. Specimens of different populations of a species with a large distribution range, like *H. axyridis*, could react differently to climate (phenotypic plasticity), caused by the genetic differences between the widely geographically separated populations. Different populations could imply different adaptations to climate. Non-melanic and melanic forms of *H. axyridis* show different responses to climates (Komai 1956) and differences in relative fitness exist between melanics and non-melanics (Soares et al. 2001, 2003) and their phenotypes (Kuang and Xiao 1995). Melanic forms would be in advantage over non-melanic forms in colder climates, melanic forms being able to attain higher body temperatures than non-melanic forms when exposed to sunlight and therefore a greater fitness (Koch et al. 2006).

The individuals introduced by INRA into Europe originate from a Chinese population (Ongagna et al. 1993). It is unknown, however, from what location in China they exactly came from ('Beijing' as cited by García et al. 1999). We have strong indications that the INRA population originates from individuals imported from north-east China because: (1) most individuals found in western Europe belong to the 'succinea' type (~80%) while 20% consists of the melanic types such as 'spectabilis' (~15%) and 'conspicua' (~5%), (2) about 95% of the individuals found in Europe, show an elytral ridge. This fits well the descriptions given by Dobzhansky (1933) and Komai et al. (1950) for north-east China and as well as those examined by I. Zakharov (March 2007, personal communication). Using the 'Match Climates' option in CLIMEX, which is independent of the species requirements, climates of different locations in north-east China (Shenyang, Tianjin, Linxi) and those in Europe show a high level of similarity (0.60 or more) with most European locations.

Compared to the European populations melanic forms are rare in North America, suggesting a different source. From what origin the North American feral populations originate (Krafsur et al. 1997), however, is not exactly known. Releases have been made in North America with offspring of populations from various imports (Korea, USSR, Japan), (ARS 2005; Gordon 1985; Table 2). Instead, because of intentional introductions from 1978 to 1982 (Teddars and Schaefer 1994), Day et al. (1994) presume that, based on its spread, initial establishment was caused by accidental seaport introductions at the port of New Orleans in Louisiana. Also in western Washington, especially near Puget Sound, an inlet used by ships headed to the ports of Seattle and Tacoma, the species is common. There, the first recovery occurred 12 years after the releases in 1981/1982 (ARS 2005). Also other authors (Krafsur et al. 1997; Koch 2003) suggested that, based on the genetic similarities between widely distributed North American populations, feral populations of *H. axyridis* in North America might have come from a single source. Both melanic and non-melanic forms were initially collected and reared in the USDA quarantine facilities, but black colour forms have been found in the Oregon and Washington states only, whereas in other parts of the United States only the 'succinea' form is present (LaMana and Miller 1998; Krafsur et al. 1997). Our predictions from CLIMEX, using the same set of parameters for both continents, however, give an adequate match with the realized distribution in both cases, suggesting that few differences exist. Morphological examination of specimens of both continents by I. Zakharov (personal communication, 2007) also indicated a large similarity. Molecular research will shed more light on the composition and differences between populations in both continents.

Geographical distribution of species

A CLIMEX-prediction is more useful for species with a restricted home range, like *H. axyridis*, than for a more cosmopolitan species. The size of a home-ranged species is clearly restricted. Subsequently it is easier to extrapolate the climate of the home range to other continents. In the case of *H. axyridis*, the situation is ideal because this species has already been introduced and established in some other continents. In this way the parameter values can be easily verified. We can use the observed distribution outside its native range as a check for the parameter values in CLIMEX. Because establishment in North America and Europe are well covered by the EI values higher than zero, and also the establishments South America are covered, it can be concluded that the parameter values in this research were appropriate.

A relatively large discrepancy remains between the current and predicted distribution in Europe. Currently the area of distribution of *H. axyridis* ranges from Denmark in the north, UK in the west, Poland in the east and Northern Italy in the south (see Brown et al. 2007). CLIMEX predicts both temperate and Mediterranean climates as being suitable for establishment of *H. axyridis* (Fig. 6). However, until now no large numbers of *H. axyridis* have been recorded from Southern Europe, in spite of multiple releases made in that area (e.g. Katsoyannos et al. 1997 in citrus). When adapting DPD values from 40 to 90 days or more, the minimum number of days below DPT0 required for diapause to be complete, the prediction in CLIMEX gave a better fit. Is it a matter of time for *H. axyridis* to expand beyond its current range or does its spread come to a halt? Climate, based on our analysis, is not a limiting factor by itself. Seasonality, however, determining certain biological and ecological features of host plants, available prey and unfavourable winter conditions, could play an important role. Though polyphagous in food acceptance, aphids are the primary food source of *H. axyridis*. Aphid pests are characteristic for temperate areas, showing large variety in species in different habitats and seasonal fluctuations. In north and central Europe aphids developing on young plant material can rapidly develop large populations in spring, summer and fall, under warm and moist conditions. In Mediterranean areas there are relatively more evergreen plants such as citrus, and summers are relatively dry, resulting in relatively less vegetative growth and long periods without substantial food sources. A second explanation for the absence of dense populations in Southern Europe is the intensity in which the landscape is used. In north-west Europe the landscape largely consist of intensively used, urban, industrial and cultivated areas. This is expressed in a dominance of annual crops and a diversity of semi-arboreal habitats. Therefore, in addition to CLIMEX, the influence of soil, vegetation type, habitat and land use should be explored for fine-tuning its potential spread.

A third explanation could be that favourable (low temperature) overwintering conditions and sites in the south are limited to certain restricted natural areas, thus limiting the winter survival by *H. axyridis* in large quantities. Adults entering diapause will stay in relative warm conditions over winter in the south of Europe (and in heated buildings in the north). They will be depleted of fat-reserves during the winter period and die before being able to allocate new prey in spring.

In conclusion, we see that according to the CLIMEX predictions, *H. axyridis* will be able to survive and establish in large parts of the world. In North America, the prediction of the model fits the current distribution very well. In Europe, where its spread is still ongoing, the area of recovery largely fits the prediction too, but its limit to the eastern and southern expansion has to be verified. On the southern hemisphere, where *H. axyridis* has recently been introduced intentionally or may arrive by accident, the chances of survival are substantial in a large part. CLIMEX estimates have proven its use as a strategic tool for pest risk assessments (Baker et al. 2000), when time and opportunities are lacking and rapid decisions have to be taken with little experimental data available. For predicting the likelihood and impact of establishment of a biological control agent such as *H. axyridis* (van Lenteren et al. 2003), it can be a first step tool in assessing risks for non-target species.

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