Diversity and Distributions, (Diversity Distrib.) (2012) **18**, 717–725

Diversity and Distributions
A Journal of Conservation Biogeography

BIODIVERSITY
RESEARCH

Invasive alien predator causes rapid declines of native European ladybirds

Helen E. Roy[1]*, Tim Adriaens[2], Nick J. B. Isaac[1], Marc Kenis[3], Thierry Onkelinx[2], Gilles San Martin[4], Peter M. J. Brown[5], Louis Hautier[6,7], Remy Poland[8], David B. Roy[1], Richard Comont[1], René Eschen[3], Robert Frost, Renate Zindel[3,9], Johan Van Vlaenderen[3], Oldřich Nedvěd[10], Hans Peter Ravn[11], Jean-Claude Grégoire[7], Jean-Christophe de Biseau[12], Dirk Maes[2]

[1]*NERC Centre for Ecology & Hydrology, Benson Lane, Crowmarsh Gifford, Oxfordshire, OX10 8BB, UK,* [2]*Research Institute for Nature and Forest (INBO), Kliniekstraat 25, B-1070 Brussels, Belgium,* [3]*CABI Europe-Switzerland, 1 Rue des Grillons, 2800 Delémont, Switzerland,* [4]*Behavioural Ecology and Conservation group, Biodiversity Research Centre, Earth and Life Institute, Universite catholique de Louvain, Croix du Sud 4, B-1348 Louvain-la-Neuve, Belgium,* [5]*Animal & Environmental Research Group, Department of Life Sciences, Anglia Ruskin University, East Road, Cambridge, CB1 1PT, UK,* [6]*Unité Protection des plantes et écotoxicologie, Département Sciences du vivant, Centre wallon de Recherches agronomiques, Rue de Liroux, 2, B-5030 Gembloux, Belgium,* [7]*Lutte biologique et Ecologie spatiale (Biological Control and Spatial Ecology Lab), CP 160/12, Université Libre de Bruxelles, 50 av FD Roosevelt, 1050 Bruxelles, Belgium,* [8]*Clifton College, 32 College Rd, Clifton, Bristol, Avon, BS8 3JH, UK,* [9]*Department of Biology, University of Fribourg, Chemin du Musée 10, 1700 Fribourg, Switzerland,* [10]*Faculty of Biological Sciences and Institute of Entomology, University of South Bohemia, Academy of Sciences of the Czech Republic, Branišovská 31, CZ-37005 České Budějovice, Czech Republic,* [11]*University of Copenhagen, Forest & Landscape, Rolighedsvej 23, DK-1958 Frederiksberg C. Denmark,* [12]*Evolution Biologique et Ecologie, Université Libre de Bruxelles, CP 160/12, Av. F.D. Roosevelt 50 – 1050 Bruxelles, Belgium*

*Correspondence: Helen E. Roy, NERC Centre for Ecology & Hydrology, Benson Lane, Crowmarsh Gifford, Oxfordshire, OX10 8BB, UK and Tim Adriaens, Research Institute for Nature and Forest (INBO), Kliniekstraat 25, B-1070 Brussels, Belgium.
E-mail: hele@ceh.ac.uk; tim.adriaens@inbo.be

ABSTRACT

Aim Invasive alien species (IAS) are recognized as major drivers of biodiversity loss, but few causal relationships between IAS and species declines have been documented. In this study, we compare the distribution (Belgium and Britain) and abundance (Belgium, Britain and Switzerland) of formerly common and widespread native ladybirds before and after the arrival of *Harmonia axyridis*, a globally rapidly expanding IAS.

Location Europe

Methods We used generalized linear mixed-effects models (GLMMs) to assess the distribution trends of eight conspicuous and historically widespread and common species of ladybird within Belgium and Britain before and after the arrival of *H. axyridis*. The distribution data were collated largely through public participatory surveys but verified by a recognized expert. We also used GLMMs to model trends in the abundance of ladybirds using data collated through systematic surveys of deciduous trees in Belgium, Britain and Switzerland.

Results Five (Belgium) and seven (Britain) of eight species studied show substantial declines attributable to the arrival of *H. axyridis*. Indeed, the two-spot ladybird, *Adalia bipunctata*, declined by 30% (Belgium) and 44% (Britain) over 5 years after the arrival of *H. axyridis*. Trends in ladybird abundance revealed similar patterns of declines across three countries.

Main conclusion Together, these analyses show *H. axyridis* to be displacing native ladybirds with high niche overlap, probably through predation and competition. This finding provides strong evidence of a causal link between the arrival of an IAS and decline in native biodiversity. Rapid biotic homogenization at the continental scale could impact on the resilience of ecosystems and severely diminish the services they deliver.

Keywords
Biological control, biological invasions, citizen science, Coccinellidae, *Harmonia axyridis*, population decline.

DOI: 10.1111/j.1472-4642.2012.00883.x
http://wileyonlinelibrary.com/journal/ddi

INTRODUCTION

Rates of global extinction are orders of magnitude higher than historical estimates and show no sign of slowing (Millenium Ecosystem Assessment, 2005). The Convention on Biological Diversity and the 10th Conference of the Parties in Nagoya (2010) identified invasive alien species (IAS) as one of the five major pressures driving biodiversity loss and ultimately extinction of species (Thomas *et al.*, 2004; Hooper *et al.*, 2005; Winter *et al.*, 2009). IAS have direct ecological effects on other species through a variety of mechanisms (Parker *et al.*, 1999). In particular, invertebrate predators may displace indigenous species by direct predation, exploitative competition for food or space, lower immunity to shared natural enemies, introduction of new pathogens or disrupted mating systems (Snyder & Evans, 2006; Kenis *et al.*, 2009).

Invasive alien species are unlike other drivers of change because the time at which an IAS arrives within an ecosystem is often known. Perhaps surprisingly then, there have been few clear demonstrations that IAS cause biodiversity loss. Vilà *et al.* (2011) provide compelling evidence, through a meta-analysis approach, that alien plant species exert significant impacts on resident plant species, communities and ecosystems. However, the majority of studies implicating IAS in species declines involve basic correlations in degraded ecosystems (Gurevitch & Padilla, 2004; Didham *et al.*, 2005) at small spatial scales and over short time-scales. Such evidence has been criticized as circumstantial, leading to suggestions that IAS might be passengers, as opposed to drivers, of change (MacDougall & Turkington, 2005). The difficulty of distinguishing between correlates and causes of population decline has been widely debated by ecologists (Ricciardi, 2004; Clavero & Garcia-Berthou, 2005; Didham *et al.*, 2005). Likewise, it is equally difficult to determine the relative importance of different causal mechanisms acting on the same system (Didham *et al.*, 2005). The correlation between the presence of the invasive alien zebra mussel, *Dreissena polymorpha* (Pallas), and decline of unionid mussels in North America (Ricciardi *et al.*, 1998; Ricciardi & Rasmussen, 1999) is unquestionable (Ricciardi, 2004), but the arrival of this particular IAS appears to be only one link in the 'chain of causality' (Didham *et al.*, 2005).

The arrival of the alien predator *Harmonia axyridis* (Pallas) in Europe provides an opportunity to investigate the distribution status of native species before and after establishment of an IAS. *Harmonia axyridis*, a native of central and eastern Asia, was released for the control of pest insects across North America from 1916 and Europe from the late 1980s (Brown *et al.*, 2008a,b). It is now considered an IAS in North America and many European countries, having undergone a period of rapid expansion, spreading in many countries without deliberate release (Brown *et al.*, 2008a,b). *Harmonia axyridis* is a large and voracious predator that threatens biodiversity because it out-competes and displaces native ladybirds and other aphidophagous insects (Majerus *et al.*, 2006; Brown *et al.*, 2011; Roy *et al.*, 2011a,b). Harmon *et al.* (2007) highlighted the dominance of alien coccinellids in aphidophagous communities across North America but concluded that it was difficult to make general conclusions as to the effect of these alien species on native coccinellid assemblages. However, the potential loss of beneficial and charismatic coccinellids is an important issue because of their role in maintaining a properly functioning ecosystem and their intrinsic aesthetic value (Department for Environment, Food and Rural Affairs, 2011).

Here, we document trends in the distribution and abundance of native ladybird species during the period of arrival and rapid expansion of *H. axyridis.* We take advantage of extensive citizen-driven field surveys in Belgium and Britain spanning decades, as well as intensive monitoring by scientists in three countries. The combination of fine-scale data collection, replicated in time (over decades and including detailed observations before and after the arrival of an IAS) and with extensive coverage in three European countries, allied with powerful modern statistical techniques, thus provides a uniquely rigorous test of the impacts of an IAS on biodiversity.

METHODS

Distribution data source: large-scale ladybird surveys

The Belgian and British checklists contain 38 and 25 native ladybird species (Baugnée *et al.*, 2011; Roy *et al.*, 2011a), respectively, from the subfamilies Chilocorinae, Coccinellinae and Epilachninae. Distribution data have been collated largely through public participatory surveys. In Britain, a Coccinellidae Recording Scheme has been run through the Biological Records Centre (NERC Centre for Ecology & Hydrology) since 1971 with an online survey launched in 2005 (Roy *et al.*, 2011a). In Belgium, the Coccinula Recording Scheme has been active since 1999 with an online survey (Baugnée *et al.*, 2011); however, *ad hoc* earlier records exist and were included in analyses. All records used in these analyses have been verified by a recognized expert. The observations are georeferenced to 1-km^2 resolution using the Ordinance Survey British national grid reference system in Britain and the Universal Transverse Mercator (UTM) in Belgium. The British and Belgian databases contain 89,994 and 67,561 observations, respectively (Table 1).

Distribution data analysis

Analyses are based on separate data sets for each country from the respective survey databases, in which each row of data corresponds to a unique combination of year and 1-km^2. The columns refer to different ladybird species, and the data are 1 (present, i.e. recorded) and 0 (absence inferred) for each species 1-km^2-year combination. The survey database contains presence-only records, and so the absence of ladybird species was inferred from the presence of others, such that if three species were recorded in a particular 1-km^2-year, we inferred that all other species were absent (Biesmeijer *et al.*, 2006). By definition, all 1-km^2-year combinations contain at least one

Table 1 Summary of ladybird distribution data in Belgium and Britain. Data were collated from volunteer recorders through national schemes: each record corresponds to an observation of a ladybird species within a 1-km^2 square in a given year. Our analyses were based on a filtered data set consisting of nine 'focal' species for which > 1000 records were available since 1990, and including only 1-km^2-year combinations that were 'well sampled'. The arrival year of *Harmonia axyridis* varies among 1-km^2, and this variation was included within the models

Species	Belgium	Britain
Total number of records (all years, all species)	67,560	89,994
Total number of surveyed 1-km^2 since 1990*	5300	14,364
Number of 1-km^2-year combinations since 1990	9889	23 929
Number of 1-km^2-year combinations used for analysis†	1419	1746
Number of 1-km^2 used for analysis†	365	411
Number of 1-km^2 with *H. axyridis*	269	249
Median year of arrival	2004	2007

*Focal species only.

†Only includes 1-km^2 with ≥ 2 focal species recorded in each of ≥ 3 years.

record (i.e. 1-km^2-year combinations with no records were assumed not to have been surveyed). We guarded against the possibility that incorrectly inferring absence might lead to spurious results by restricting our analyses to a small number of 'focal' species in 'well-sampled' 1-km^2. Focal species are those for which there were > 1000 observations per country since 1990 (nine species, *Adalia bipunctata*, *Adalia decempunctata*, *Calvia quatuordecimguttata*, *Coccinella septempunctata*, *Exochomus quadripustulatus*, *Halyzia sedecimguttata*, *Propylea quattuordecimpunctata*, *Psyllobora vigintiduopunctata* and *H. axyridis* in each country). All ladybird species included were conspicuous and historically widespread and common (Roy *et al.*, 2011a), and so we were confident in inferring absence of a species on the basis of the presence of other species. We defined 'well-sampled' combinations as those in which at least two focal species were observed. Furthermore, we included only 1-km^2 that were 'well sampled' in at least 3 years. These criteria restricted our data set to the small proportion (7% in Britain, 14% in Belgium) of high-quality data (Table 1). We repeated our analyses with different thresholds for the definition of 'well sampled', but the results were qualitatively unchanged (Supplementary Table S1).

To analyse the distribution data, we used generalized linear mixed-effects models (GLMMs) with binomial errors and logit link function. For each species and country, we modelled the probability of 1-km^2 occupancy (presence versus absence) as the sum of two linear trends, Y and H. Parameter Y is the linear occupancy trend in the absence of *H. axyridis*, estimated using a fixed effect of year centred on the time of *H. axyridis* arrival in the respective country (2001 in Belgium and 2004 in Britain). Parameter H estimates the net effect of *H. axyridis* in that 1-km^2 (years prior to arrival and 1-km^2 that were never colonized were coded as zero). Thus, for a British grid cell that was colonized by *H. axyridis* in 2007, the fitted value for 2009 is given by the intercept plus 5^*Y plus 2^*H. The model fits the probability of occupancy on the logit scale. Our null hypothesis for each species is that parameter H is equal to zero. We included 1-km^2 as random intercept and year as random slope (to allow for different trends in each 1-km^2), as well as an observation-level random effect to account for overdispersion. All models were fitted in R 2.11.1 (Ihaka & Gentleman, 1996) with the lme4 package version 0.999375-37 (Bates & Maechler, 2010).

Systematic surveys of ladybird abundance

Ladybird abundance data were collected using systematic fortnightly surveys in Brussels (Belgium) during spring 2003, 2005 and 2008, in lime (*Tilia* × *vulgaris* Hayne) and sycamore (*Acer pseudoplatanus* L.) trees in 12 urban localities (parks, avenues and roadsides). Surveys at four sites in Cambridgeshire (Britain) and 15 sites in north-western Switzerland span 2006–2010: each site was surveyed 7–9 times per year between April and October. All Cambridgeshire sites were in suburban locations and consisted primarily of deciduous trees; Swiss sites were 50 m sections of mixed deciduous hedges. In all countries, surveys were conducted using standard sampling methods including tree-beating and sweep-netting (Adriaens & Maes, 2004; Eschen *et al.*, 2007; Brown *et al.*, 2011). At all sites, branches were beaten with a stick (approximately 1 m) above a beating tray (variable diameter for each country ranging from 0.65 to 1.25 m). At each of the Brussels sites, 100 branches were sampled in deciduous trees. This sampling was performed across 10 randomly selected trees within each site. In Switzerland, data were obtained from hedgerows consisting of mixed deciduous woody species (either planted hedges or forest edge), and the branches of all shrubs and trees up to a height of 3.5 m were sampled. In the Cambridgeshire sites deciduous trees were sampled for a fixed time period (20–60 min depending on the area of the site). Adults of all ladybirds were counted and identified before being released on-site.

Population data analysis

We modelled the abundance of each species at our systematic survey sites in each country separately, including only ladybird species associated with deciduous trees and for which at least 50 individual lady birds were captured. We also modelled the total abundance of all native species and the total number of species. We used GLMMs with Poisson errors and log link with the year centred on the year of the arrival of *H. axyridis* (2001 in Belgium, 2004 in Britain and 2006 in Switzerland) as a fixed effect. The random effects included site, visit and observation (to account for overdispersion).

RESULTS

Distribution data: large-scale ladybird surveys

The median year of arrival of *H. axyridis* in Belgium was 2004 and in Britain 2007 (Table 1). *Harmonia axyridis* colonized at least 269 of the 365 1-km^2 (74%) analysed for Belgium and 249 of the 411 1-km^2 (61%) analysed for Britain (Table 1). In the absence of *H. axyridis*, similar numbers of species expanded and contracted their British ranges, whereas in Belgium, there were more species expanding than contracting (Table 2; Fig. 1). *Harmonia axyridis* had a significant negative impact ($H < 0$) on the distribution of five species in Belgium and all but one of the eight species in Britain (Table 2). The magnitude of these effects is large, that is, $|H| > |Y|$, such that these species have shown substantial range retraction (Table 2; Fig. 1). This is exemplified by *A. bipunctata*, which declined by 30% in Belgium and 44% in Britain over the five years following the arrival of *H. axyridis* (Fig. 2). A few ladybirds were declining prior to the arrival of *H. axyridis* ($Y < 0$), but *H. axyridis* has significantly accelerated the rate of this decline.

Systematic surveys of ladybird abundance

Population trends, revealed by data from systematic surveys at specific sites in Belgium, Britain and Switzerland, strongly supported the distribution trends (Table 3). One species (*A. bipunctata*) showed significant declines in abundance in all three countries, and another species (*E. quadripustulatus)* showed significant declines in two countries (Britain and Switzerland). Three species showed significant declines in only one of the three countries (Table 3). All three countries showed a significant increase in the abundance of *H. axyridis* (Table 3), whilst at the same time, the total ladybird abundance (excluding *H. axyridis*) declined significantly in all three countries.

DISCUSSION

Here, we have assessed the effects of the arrival of an IAS on the distribution and abundance of native species across European countries. Our results clearly indicate that native ladybirds have declined markedly in response to the arrival of *H. axyridis*. This finding provides strong evidence of a causal link between the arrival of an IAS and decline in native biodiversity.

The decline in the distribution and abundance of previously widespread and common native ladybirds after the arrival of *H. axyridis* is striking. The dramatic decline of *A. bipunctata* over the five years following the arrival of *H. axyridis* is of particular note. This species is now near the threshold of detection, in both Europe (Brown *et al.*, 2011) and North America (Harmon *et al.*, 2007), in habitats in which it was previously common. *Harmonia axyridis* appears to be displacing those native ladybirds with which it shares a high niche overlap (Adriaens *et al.*, 2008), such as *A. bipunctata*. The likely mechanisms are both intra-guild competition and predation based on asymmetry of body size (*H. axyridis* is about 1.5 times larger than *A. bipunctata*) and superior physical and chemical defences in comparison with other species of ladybird (Pell *et al.*, 2008; Roy *et al.*, 2008). Laboratory studies have indicated the potential of *H. axyridis* to act as a unidirectional intra-guild predator of entomopathogenic fungi (Roy *et al.*, 2008), coccinellids (Ware & Majerus, 2008; Ware *et al.*, 2009) and other invertebrates (Koch & Galvan, 2008; Roy *et al.*, 2011a). Additionally, a recent field study, in which exogeneously sequestered alkaloids were used as a tool for detecting the consumption of other coccinellids, revealed a high prevalence of intra-guild predation (Hautier *et al.*, 2008, 2011) by *H. axyridis*. In some sites, more than 30% of *H. axyridis* larvae contained the alkaloids adaline, calvine or propyleine representing intra-guild predation of *Adalia* spp., *Calvia* spp. and *P. quattuordecimpunctata* (Hautier *et al.*, 2011).

Table 2 Trends in the distribution of European ladybirds before and after the arrival of the invasive alien predator *Harmonia axyridis*. Numbers are parameters extracted from mixed-effects models for each species based on 1419 and 1746 observations (1-km^2-year combinations) for Belgium and Britain, respectively.

	Belgium				Britain			
Species	%	*a*	*Y*	*H*	%	*a*	*Y*	*H*
Harmonia axyridis	42	−2.160	–	0.826***	25	−18.191	–	9.540***
Adalia bipunctata	52	0.521	−0.106***	−0.216***	68	1.294	0.059***	−0.535***
Adalia decempunctata	22	−1.251	0.051**	−0.187**	32	−0.888	−0.024	−0.330***
Calvia quatuordecimguttata	28	−0.975	0.013	−0.139*	21	−1.775	−0.051*	−0.205*
Coccinella septempunctata	78	1.392	0.002	0.014	75	1.403	−0.016	−0.092
Exochomus quadripustulatus	24	−1.556	0.078**	−0.187**	33	−1.032	0.091***	−0.216**
Halyzia sedecimguttata	25	−1.458	0.125***	−0.085	22	−1.532	0.200***	−0.396***
Propylea quattuordecimpunctata	55	0.336	−0.018	−0.104*	41	−0.405	−0.045**	−0.307***
Psyllobora vigintiduopunctata	40	−0.504	−0.021	0.033	28	−1.312	−0.070***	−0.285***

%: percentage of observations where the species is present, *a*: intercept (logit probability at year of first introduction), *Y*: trend in the absence of *H. axyridis* and *H*: effect of the presence of *H. axyridis* on the trend.

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

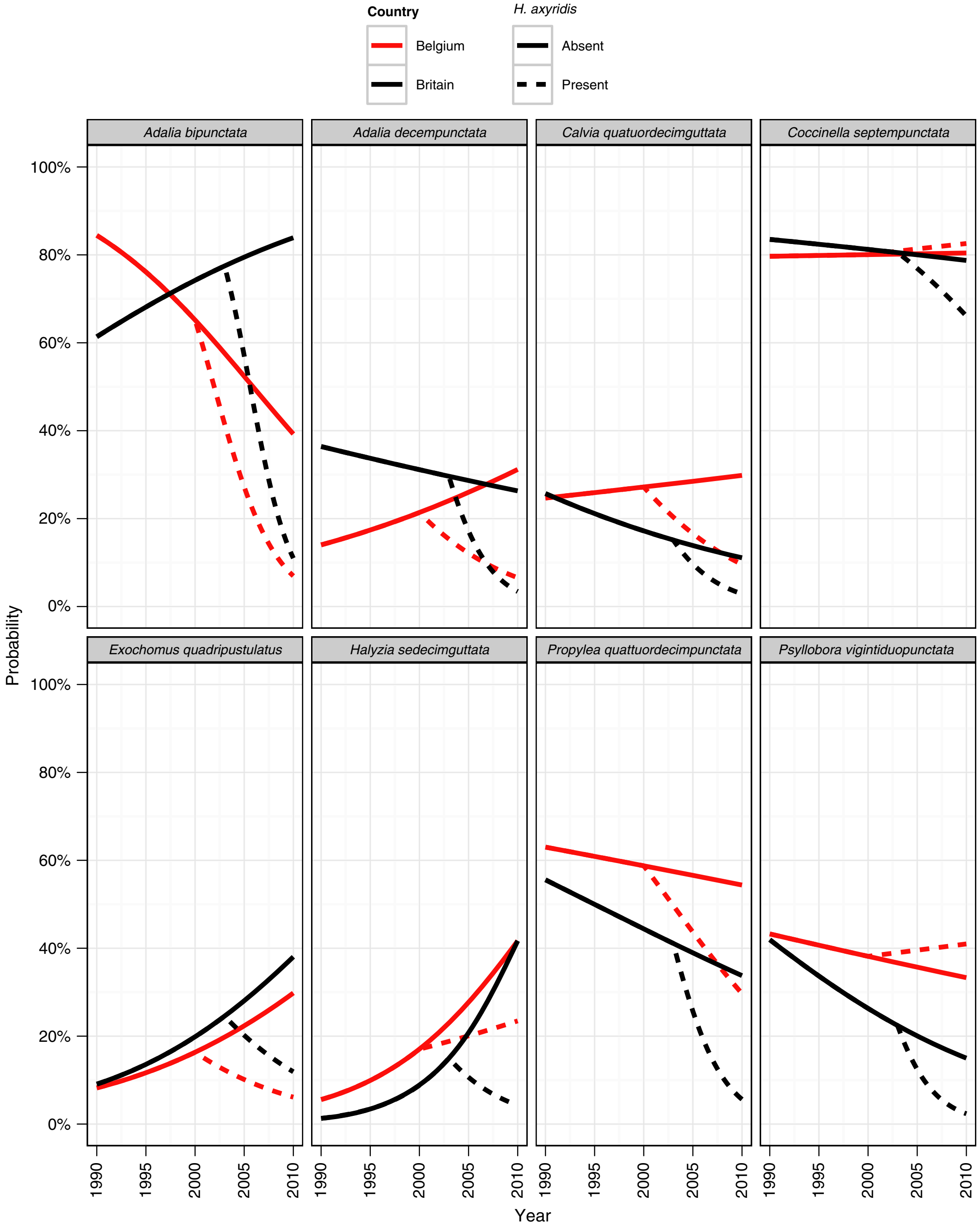

Figure 1 Effects of *Harmonia axyridis* on the distribution of eight native ladybirds based on predictions for an average 1-km^2. Prediction is based on the fixed effects of the models and ignores random variation in occupancy among specific 1-km^2. Absent assumes the 1-km^2 is not colonized by *H. axyridis*, and present assumes the 1-km^2 was colonized in 2001 (Belgium) or 2004 (Britain) by *H. axyridis*. Note that our predictions are shown in the measurement scale (probability of occupancy), rather than the modelled scale (logit).

Halyzia sedecimguttata (L.) is a mycophagous ladybird and is, unlike most of the species within our study, not in competition with *H. axyridis* for food. This ladybird has undergone a dramatic increase in abundance and distribution in Britain (Roy *et al.*, 2011a) and Belgium, which reflects a recent shift in habitat preference, previously associated with oak it is now also commonly found feeding on mildew of ash and sycamore trees (Roy *et al.*, 2011a). It is possible that climate warming has increased the availability of mildew for this mycophagous species. However, this trend is reversed in Britain in the presence of *H. axyridis*. The feeding niches of *H. axyridis* and *H. sedecimguttata* do not overlap, but their habitats do. *Halyzia sedecimguttata* is likely to be particularly vulnerable to predation by *H. axyridis* in the autumn when, unlike most ladybird species, *H. sedecimguttata* and *H. axyridis* exist predominantly as larvae and pupae (immature stages). At

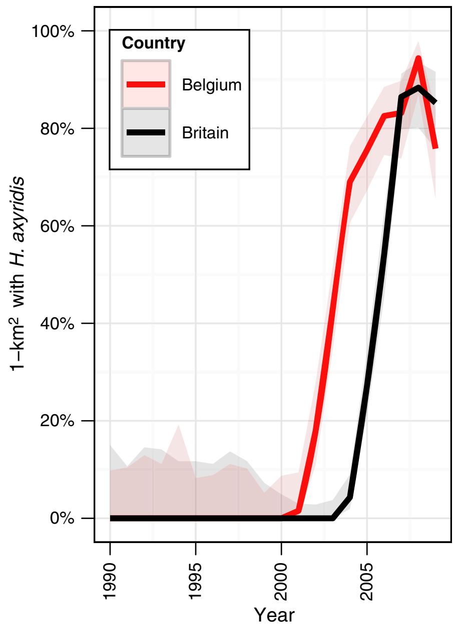

Figure 2 Invasion of Belgium and Britain by *Harmonia axyridis*, expressed as the percentage of all 'well-sampled' 1-km^2 that were colonized. The diffuse ribbons delimit the 95% confidence intervals.

this time, the aphids, the main prey of *H. axyridis*, are in decline, and so alternative prey including the immature stages of other insects such as *H. sedecimguttata* is consumed (Brown *et al.*, *2011*). It is likely that subtle differences in the phenology of ladybirds within Belgium and Britain alter the interactions between species.

One species, *C. septempunctata*, within our study provides a particularly interesting contrast in that its distribution and abundance appear to be stable across Europe despite the arrival of *H. axyridis*. This common ladybird is mainly associated with herbaceous vegetation (Roy *et al.*, 2011a) and so does not overlap with *H. axyridis* to the extent of the four tree specialists (*A. bipunctata*, *A. decempunctata*, *C. quattuordecimguttata* and *E. quadripustulatus*). Additionally, *C. septempunctata* is a large ladybird, of similar size to *H. axyridis*. *Coccinella septempunctata* is itself a successful IAS in the USA and Canada, where it is thought to have contributed to declines in native species (Harmon *et al.*, 2007).

Historically, the decline of widespread and common species has gone largely unnoticed, and there is a paucity of quantitative information on such declines (Gaston & Fuller, 2007; Van Dyck *et al.*, 2009), especially among invertebrates. The pronounced decline of species widely regarded as unthreatened (none of the declining species are categorized according to IUCN conservation designations) highlights the importance of continued large-scale monitoring of both rare and common species within the wider countryside. The decline in ladybird species across Europe and associated alterations to community composition could have far-reaching effects on ecosystem services (Hooper *et al.*, 2005). Predatory ladybirds are known to provide a major ecosystem service by regulating pest insects. Although *H. axyridis* is an effective biological control agent in crop systems (Tedders & Schaefer, 1994; Brown & Miller, 1998; Alyokhin & Sewell, 2004; Heimpel *et al.*, 2010), it is unclear whether it can fulfil all the functional roles of the species it is displacing. *Harmonia axyridis* is rapidly expanding its global range: our results imply that this will cause ecological extinctions (Estes *et al.*, 1989) of native species, notably deciduous tree specialists, over large areas.

There is considerable debate over the relationship between species diversity and ecosystem processes. It is apparent that species diversity enhances productivity and stability in some ecosystems, but not in others (Johnson *et al.*, 1996; Rey

Table 3 Trends in the abundance of European ladybirds at a number of deciduous tree sites within Britain, Belgium and Switzerland after the arrival of the invasive alien predator *Harmonia axyridis*. The systematic surveys were repeated 7–9 times per field season (April–October). Numbers are parameters extracted from mixed-effects models for each species

	Britain		Belgium		Switzerland	
Species	*n*	Trend	*n*	Trend	*n*	Trend
H. axyridis	1 824	1.278***	2 651	0.550***	1 344	0.894***
Adalia bipunctata	931	−0.472***	689	−0.877***	293	−0.571**
Adalia decempunctata	1 702	−0.169*	198	−0.125	356	−0.058
Calvia quatuordecimguttata	249	0.031	145	0.035	138	−0.272
Coccinella septempunctata	1 557	0.193	–	–	–	–
Exochomus quadripustulatus	753	−0.200*	160	−0.192	83	−0.957***
Halyzia sedecimguttata	–	–	126	0.397***	–	–
Propylea quattuordecimpunctata	428	−0.039	66	−0.142	251	−0.629***
Calvia decemguttata	–	–	179	−0.091	–	–
Oenopia conglobata	–	–	125	−0.623***	–	–
Total (all native species)	10,793	−0.091*	1711	−0.220***	1376	−0.465***
Number of native species	16	−0.028	12	−0.084**	18	−0.329***

n, number of individual ladybirds.
$^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

Benayas *et al.*, 2009). However, it is often difficult to predict which species are critical to functioning or provide resilience and resistance to environmental changes. Additionally, the arrival of an IAS (or, indeed, other anthropogenic perturbation) is more likely to change the relative abundance of species rather than result in extinction of a species, but the relationship between community composition (species richness) and ecosystem functioning has focussed on effects of species extinctions (Chapin *et al.*, 2000). We predict that the dominance of *H. axyridis*, and associated reduction of diversity, will decrease the resilience of aphidophagous guilds and severely diminish the services they deliver (Biesmeijer *et al.*, 2006; Winter *et al.*, 2009).

ACKNOWLEDGEMENTS

The late Professor Michael Majerus, our colleague and friend from the University of Cambridge, was instrumental in establishing this research collaboration. The authors are extremely grateful to the many thousands of people across Belgium and Britain who have contributed their ladybird findings to the surveys. Their enthusiasm has been inspirational. H.E.R., N.I. and D.B.R. are funded through the NERC Centre for Ecology & Hydrology and the Joint Nature Conservation Committee. The development of the online surveys in Britain was in part through funding received from the Department for Environment, Food and Rural Affairs (Defra). We are grateful to Natuurpunt and Natagora for providing the online encoded records of ladybirds in Belgium. Research in Switzerland was funded by a grant from the Swiss Federal Office for the Environment (F232-0377) and the EU FP6 project ALARM (GOCE-CT-2003-506675). ON was funded by grant numbers QH82047 by the Ministry of Agriculture and 6007665801 by the Ministry of Education of the Czech Republic. HPR was funded through the Villum Foundation.

REFERENCES

Adriaens, T. & Maes, D. (2004) Voorlopige verspreidingatlas van lieveheersbeestjes in Vlaanderen. *Bertram*, **1bis**, 1–71.

Adriaens, T., Gomez, G.M.Y. & Maes, D. (2008) Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium. *BioControl*, **53**, 69–88.

Alyokhin, A. & Sewell, G. (2004) Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions*, **6**, 463–471.

Bates, D. & Maechler, M. (2010) *lme4: linear mixed-effects models using S4 classes*. R package version 0.999375-37. Available at: http://CRAN.R-project.org/package=lme4 (accessed 12 November 2010).

Baugnée, J.-Y., Branquart, E., Maes, D. & Segers, S. (2011) *Velddeterminatietabel voor de lieveheersbeestjes van België en Nederland (Chilocorinae, Coccinellinae, Epilachninae & Coccidulinae): herziene druk met larventabel*. Jeugdbond voor Natuur en Milieu (Gent), Jeunes & Nature asbl (Wavre) i.s.m. het Instituut voor Natuur- en Bosonderzoek, (Brussel).

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Brown, M.W. & Miller, S.S. (1998) Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the impact of invasion by *Harmonia axyridis*. *Entomological News*, **109**, 143–151.

Brown, P.M.J., Adriaens, T., Bathon, H., Cuppen, J., Goldarazena, A., Hagg, T., Kenis, M., Klausnitzer, B.E.M., Kovar, I., Loomans, A.J.M., Majerus, M.E.N., Nedvěd, O., Pedersen, J., Rabitsch, W., Roy, H.E., Ternois, V., Zakharov, I.A. & Roy, D.B. (2008a) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *BioControl*, **53**, 5–21.

Brown, P.M.J., Roy, H.E., Rothery, P., Roy, D.B., Ware, R.L. & Majerus, M.E.N. (2008b) *Harmonia axyridis* in Great Britain: analysis of the spread and distribution of a non-native coccinellid. *BioControl*, **53**, 55–67.

Brown, P.M.J., Frost, R., Doberski, J., Sparks, T., Harrington, R. & Roy, H.E. (2011) Decline in native ladybirds in response to the arrival of *Harmonia axyridis* (Coleoptera: Coccinellidae): early evidence from England. *Ecological Entomology*, **36**, 231–240.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234–242.

Clavero, M. & Garcia-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution*, **20**, 110–110.

Department for Environment Food and Rural Affairs (2011) *The Natural Choice: securing the value of nature. (ed Defra)*. The Stationery Office Limited, London.

Didham, R.K., Tylianakis, J.M., Hutchison, M.A., Ewers, R.M. & Gemmell, N.J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, **20**, 470–474.

Eschen, R., Babendreier, D., Nauer, S., Bigler, F. & Kenis, M. (2007) Surveys for ladybirds (Coleoptera :Coccinellidae) in Switzerland and confirmation of the presence of the invasive alien ladybird species, Harmonia axyridis (Pallas). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **80**, 7–14.

Estes, J.A., Duggins, D.O. & Rathbun, G.B. (1989) The ecology of extinctions in kelp forest communities. *Conservation Biology*, **3**, 252–264.

Gaston, K.J. & Fuller, R.A. (2007) Biodiversity and extinction: losing the common and the widespread. *Progress in Physical Geography*, **31**, 213–225.

Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, **19**, 470–474.

Harmon, J.P., Stephens, E. & Losey, J. (2007) The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *Journal of Insect Conservation*, **11**, 85–94.

Hautier, L., Gregoire, J.-C., de Schauwers, J., Martin, G.S., Callier, P., Jansen, J.P. & de Biseau, J.-C. (2008) Intraguild predation by *Harmonia axyridis* on coccinellids revealed by exogenous alkaloid sequestration. *Chemoecology*, **18**, 191–196.

Hautier, L., San Martin, G., Callier, P., de Biseau, J.-C. & Grégoire, J.-C. (2011) Alkaloids provide evidence of intraguild predation on native coccinellids by Harmonia axyridis in the field. *Biological Invasions* **13**, 1805–1814.

Heimpel, G.E., Frelich, L.E., Landis, D.A., Hopper, K.R., Hoelmer, K.A., Sezen, Z., Asplen, M.K. & Wu, K.M. (2010) European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. *Biological Invasions*, **12**, 2913–2931.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.

Johnson, K.H., Vogt, K.A., Clark, H.J., Schmitz, O.J. & Vogt, D.J. (1996) Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology & Evolution*, **11**, 372–377.

Kenis, M., Auger-Rozenberg, M.A., Roques, A., Timms, L., Pere, C., Cock, M., Settele, J., Augustin, S. & Lopez-Vaamonde, C. (2009) Ecological effects of invasive alien insects. *Biological Invasions*, **11**, 21–45.

Koch, R.L. & Galvan, T.L. (2008) Bad side of a good beetle: the North American experience with *Harmonia axyridis*. *BioControl*, **53**, 23–35.

MacDougall, A.S. & Turkington, R. (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42–55.

Majerus, M.E.N., Slawson, V. & Roy, H.E. (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecological Entomology*, **31**, 207–215.

Millenium Ecosystem Assessment(2005) *Ecosystems and human well-being: current state and trends*. World Resources Institute, Washington, DC.

Parker, I., Simberloff, D., Lonsdale, W., Goodell, K., Wonham, M., Kareiva, P., Williamson, M., Von Holle, B., Moyle, P., Byers, J. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Pell, J.K., Baverstock, J., Roy, H.E., Ware, R.L. & Majerus, M.E.N. (2008) Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. *BioControl*, **53**, 147–168.

Rey Benayas, J.M., Newton, A.C., Diaz, A. & Bullock, J.M. (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science*, **325**, 1121–1124.

Ricciardi, A. (2004) Assessing species invasions as a cause of extinction. *Trends in Ecology & Evolution*, **19**, 619–619.

Ricciardi, A. & Rasmussen, J.B. (1999) Extinction rates of North American freshwater fauna. *Conservation Biology*, **13**, 1220–1222.

Ricciardi, A., Neves, R.J. & Rasmussen, J.B. (1998) Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology*, **67**, 613–619.

Roy, H.E., Baverstock, J., Ware, R.L., Clark, S.J., Majerus, M.E.N., Baverstock, K.E. & Pell, J.K. (2008) Intraguild predation of the aphid pathogenic fungus *Pandora neoaphidis* by the invasive coccinellid *Harmonia axyridis*. *Ecological Entomology*, **33**, 175–182.

Roy, H.E., Brown, P.M.J., Frost, R. & Poland, R.L. (2011a) *Atlas of the Ladybirds (Coccinellidae) of Britain and Ireland*. Biological Records Centre, Wallingford.

Roy, H.E., Roy, D.B. & Roques, A. (2011b) Inventory of alien arthropod predators and parasites established in Europe. *BioControl*, **56**, 477–504.

Snyder, W.E. & Evans, E.W. (2006) Ecological effects of invasive arthropod generalist predators. *Annual Review of Ecology Evolution and Systematics*, **37**, 95–122.

Tedders, W.L. & Schaefer, P.W. (1994) Release and establishment of Harmonia axyridis (Coleoptera, Coccinellidae) in the South-eastern United States. *Entomological News* **105**, 228–243.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879–1881.

Van Dyck, H., Van Strien, A.J., Maes, D. & Van Swaay, C.A.M. (2009) Declines in Common, Widespread Butterflies in a Landscape under Intense Human Use. *Conservation Biology*, **23**, 957–965.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.

Ware, R.L. & Majerus, M.E.N. (2008) Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*. *BioControl*, **53**, 169–188.

Ware, R.L., Yguel, B. & Majerus, M.E.N. (2009) Effects of competition, cannibalism and intra-guild predation on larval development of the European coccinellid *Adalia bipunctata* and the invasive species *Harmonia axyridis*. *Ecological Entomology*, **34**, 12–19.

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didziulis, V., Hejda, M., Hulme, P.E., Lambdon, P.W., Pergl, J., Pyšek, P., Roy, D.B. & Kuhn, I. (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences USA*, **106**, 21721–21725.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article:

Table S1 Distributional trends for eight native ladybird species, using different thresholds for including data in the analysis. *n*Yr is the number of years in which a 1-km^2 needed to be 'well-surveyed' in order to be considered in the analysis. *n*Focal is the threshold number of focal species (including *Harmonia axyridis*) to consider a 1-km^2 'well-surveyed' in any 1 year. Setting both thresholds to zero includes all possible combinations, including those based on incidental records from poorly-sampled areas. Setting $n\mathrm{Yr} = 3$ and $n\mathrm{Focal} = 2$ (the penultimate model for each species) correspond to the results shown in the main document. Columns b(Y), z(Y) and p(Y) are the slope, effect size and *P*-value for the trend in the absence of *H. axyridis*; b(H), z(H) and p(H) are comparable values for the effect of *H. axyridis* on the distribution trend. *n* is the sample size (number of 1-km^2-year combinations) generated by the thresholds applied; obs is the number of combinations in which the focal species was present.

BIOSKETCH

Helen E. Roy is an ecologist leading zoological research in the Biological Records Centre at the NERC Centre for Ecology & Hydrology (UK). The focus of her research is insect community interactions with particular emphasis on the effects of environmental change. She has worked extensively on ladybirds for the last 18 years and is the volunteer scheme organizer for the UK Ladybird Survey which collates distribution data on all species of ladybird within Britain. She recently published the *Ladybirds (Coccinellidae) of Britain and Ireland*. She has an interest in biological invasions and is leading the development of the GB Non-Native Species Information Portal. She is also convenor of the IOBC WPRS Working Group 'Benefits and Risks of Exotic Biological Control Agents' and an associate editor of BioControl.

Author contributions: H.E.R., T.A. and M.K. led data collection and collation. N.J.B.I., T.O. and D.M. assembled the data and performed the analyses with assistance from H.E.R., L.H., R.C. and G.S.M. H.E.R., T.A., R.P. and P.M.J.B. collated the national distributional data. P.M.J.B., R.F., G.S.M., L.H., J.-C.G., J.-C.B., R.E., J.V.V., R.Z. and M.K. conducted the field surveys resulting in abundance data. H.E.R. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Editor: Franz Essl